The Birds, the Bees & the Bushmen: Guiding behaviour of the Greater Honeyguide, *Indicator indicator*, and its presence in the scientific literature

Anna Kingston

BSc Biology

University of Sussex, UK

Supervisor: Professor Jonathan Bacon

Dean of Life Sciences, University of Sussex, UK

April 2011 [Including 2022 erratum p45]

Acknowledgements

I would like to thank the many correspondents in Africa, America and the UK who were so happy to share their knowledge on honeyguides and guiding with me.

Special thanks goes to Hussain Isack and Claire Spottiswoode for their encouragement and their expertise on honeyguide guiding and to Andrea & Redouan Bshary for the equivalent in reef fish guiding; also to Malcolm Smith for allowing me access to his pre-publication book *Life With Birds,* to Luca Borghesio of Birdlife International for sharing with me the results of his interviews with Kikuyu tribe members on honeyguide guiding, to all at *Ostrich, British Birds* and *African Wildlife* for making difficult-to-access honeyguide articles available to me and to Mireschen Troskie-Marx and Jan-Ad Stemmet of Mimosa Films for their kind help in finding out whether the footage of a honey badger being guided by a Greater Honeyguide in the film *Animals Are Beautiful People* was of genuine or contrived behaviour.

Thanks also to Kabelo Senystso of Birdlife Botswana for providing me with a quote concerning Birdlife Botswana's position on behavioural conservation of the Greater Honeyguide's guiding, to Keith Betton, chairman of the African Bird Club, (ABC) for doing some of my work for me by emailing over 1000 members of the ABC for their experiences with honeyguides, to Elli Leadbeater and Jonathan Green of Sussex University undertaking on my behalf to question delegates of the Association for the Study of Animal Behaviour's Winter Meeting 2010 on their awareness of honeyguide guiding behaviour and to Paul Latham for making his field notes on *Indicator indicator* available to me.

Last, but of course not least, I'd like to thank my University of Sussex supervisor, Jonathan Bacon, not only for all the cups of tea, but also for his unerring enthusiasm for a project which by no means fell into his direct area of work – thank you.

Contents

The Birds, the Bees & the Bushmen: Guiding behaviour of the Greater Honeyguide, *Indicator indicator*, and its presence in the scientific literature

Abstract

Mutualisms are modernly regarded as underpinning biological and ecological processes, and can occur both internally between host and endosymbiont and externally between two free-living organisms. An example of the latter is the service-service mutualism occurring between the Greater Honeyguide (Aves: *Indicator indicator*) and humans in which the beeswax-eating bird guides humans to wild honeybee hives that it cannot itself access but that humans may break into. Examples of facultative mutualisms requiring so much coordination between partners are rare, making this an important case for study, yet *I.indicator* guiding appears infrequently in the primary literature. A literature analysis was conducted to ascertain the reasons for this and an attempt made to assemble into one place the research findings of literature retrieved. Gaps in our current knowledge of the guiding habit were also determined for directing future research. 120 publications were retrieved and their attributes, such as subject, year of publication, journal impact factor, number of times cited and accessibility rating, were converted into a multiple-field database. 70% of honeyguide literature was found to be unavailable electronically, 71% was never cited by other work, and 60% appeared in journals with an impact factor of zero, indicating that most honeyguide research would not be readily accessible or exposed to a researcher interested in the study of mutualisms or interspecific communication. Four major areas of inadequate scientific knowledge were identified and recommended for further study.

Introduction

From nectar-gaining pollinators enabling the dispersal of flowering plants' gametes to the exchange of essential amino-acids between endosymbiotic proteobacteria and their insect hosts (Nakabachi 2005), mutualisms, or 'reciprocal exploitations that provide net benefits to each partner' (Herre *et al* 1999), are increasingly being recognised as fundamental to the workings of life at both a community and cellular level (Bronstein 1994). Being part of a mutualism necessarily requires the exchange of resources or services to provide each party with something it could not obtain, or could obtain less of, on its own. In some cases, communication may be required to facilitate the commencement or optimisation of the partnership, communication that in true interspecific mutualism, rather than its intraspecific form, cooperation, must be intelligible to two different species. Since organisms can tend to be more attuned or responsive to conspecific signals than heterospecific ones (e.g. Parker & Shulman 1986; Dawson & Chittka 2010; Graver, Graver & Otter 2010), this raises an interesting challenge to the evolution of such communicative behaviour.

Numerous different species are known to exhibit some form of interspecific communication, conducted over one or more modalities from a larger possible range; some birds communicate visually with their predators by tail flashing to signal threat awareness and deter pursuit (e.g. Murphy 2006); many plants communicate toxicity to potential herbivores via the release of off-putting volatile chemicals (e.g. Pichersky & Gershenzon 2002); ants farming the larvae of riodinid butterflies are called to the aid of their predator-threatened livestock by the caterpillars' mimicry of ant alarm calls (DeVries 1992).

One of the most complex cases of interspecific communication, and thus one of the most potential interest to both behaviourists and evolutionists, is that manifested in the mutualism between the Greater Honeyguide (*Indicator indicator*) and humans. Of further note is that this relationship is mainly one of reciprocal service provision, a type of mutualism which is more uncommon (for reasons yet to be elucidated) than are resource-based or mixed exchanges (Ollerton 2006), though the resource of food is the final goal for both parties.

The honeyguides are a family of Sub-Saharan and Sub-Himalayan birds cladistically allied with the woodpeckers, toucans and barbets (see **figure 1** for distribution maps and pictures of the bird). All genera are brood parasites, and most species, to varying degrees, utilise wax as a significant source of energy intake in their diet – a practice termed 'cerophagy'. Some, such as *Prodotiscus* spp. merely ingest the waxy cuticles of insects and berries and are able to metabolise this wax to a greater extent than seen in most birds (Friedmann & Kern 1976; Diamond & Place 1988; Downs, van Dyck & Iji 2002). Others, such as members of the genus *Indicator*, actively search out bee colonies and risk the angry stings of workers in order to raid the nest for beeswax. The Greater Honeyguide is the largest of all honeyguides and has been thought too massive to gain entry to a significant proportion of bees' nest entrance holes (Friedmann 1955; Isack 1987; Short & Horne 2001). Whether because of this or because of the ability of humans to decrease bee aggression using smoke, this species has developed a fascinating mutualism with African tribes-people that involves leading, or 'guiding', the target human to a bees' nest (which may be over 1 kilometre away – Short & Horne 2001), waiting in the hive's vicinity until human access is gained by force (axes are a popular tool of choice) and the bees made torpid with woodsmoke, then either obtaining bee comb from the detritus left after human honey collection has finished or receiving it via actively offered reward from a grateful human mutualist (Skead 1951; Friedmann 1955; Macpherson 1975; Isack 1987; Isack & Reyer 1989; Short & Horne 2001). Thus the bird may obtain previously difficult to access wax through the hive-opening and bee-smoking service rendered by the human, and the human may reduce foraging time for honey – by up to 64% compared with an unaided search (Isack & Reyer 1989) – via the bird's guiding service.

Since honey is much prized by people living in areas where sugar is expensive or shops are hard to reach, this avian 'fairy godmother' is a welcome aide to people living a subsistence lifestyle. Honey gathering can even bring in enough money to fund education for a family's children. Birdlife International ornithologist, Luca Borghesio, recenty interviewed Robert Lentaaya, a member of the north Kenyan Ndoboro tribe who utilises honeyguides in his honey-hunting, who told him:

"I collect about 10 litres of honey in a year and sell it for about 2000 Kenyan shillings [£17] so I can pay for school fees for my children" [in Smith, 2011].

In successfully carrying out the communicative process involved in making this mutually beneficial relationship work, several cognitive events must be performed by each partner. On *I.indicator's* part, it must: i) recognise a potential recruit, ii) cognitively associate guiding with a food reward, iii) correctly perform display calling and posturing to successfully initiate a guiding session (and correctly terminate it once at a bees' nest), and iv) perform guiding to a bee's nest in a form humans are able to follow. The human partner's response must be to i) recognise the acoustic (harsh chattering) and visual (tail flicking and wing fluttering) displays of *I.indicator* as being indicative of a desire to guide, ii) cognitively associate guiding with a food reward, iii) subsequently follow the bird to the target bees' nest, and iv) recognise that termination of the characteristically punctuated guiding flight combined with a decrease in volume of acoustic display by the bird signals the arrival at the hive vicinity (Skead 1951; Friedmann 1955; Macpherson 1975; Isack 1987; Isack & Reyer 1989; Short & Horne 2001). Alternatively, I.indicator can be induced to guide by whistling or knocking together of sticks by a human wishing to be guided.

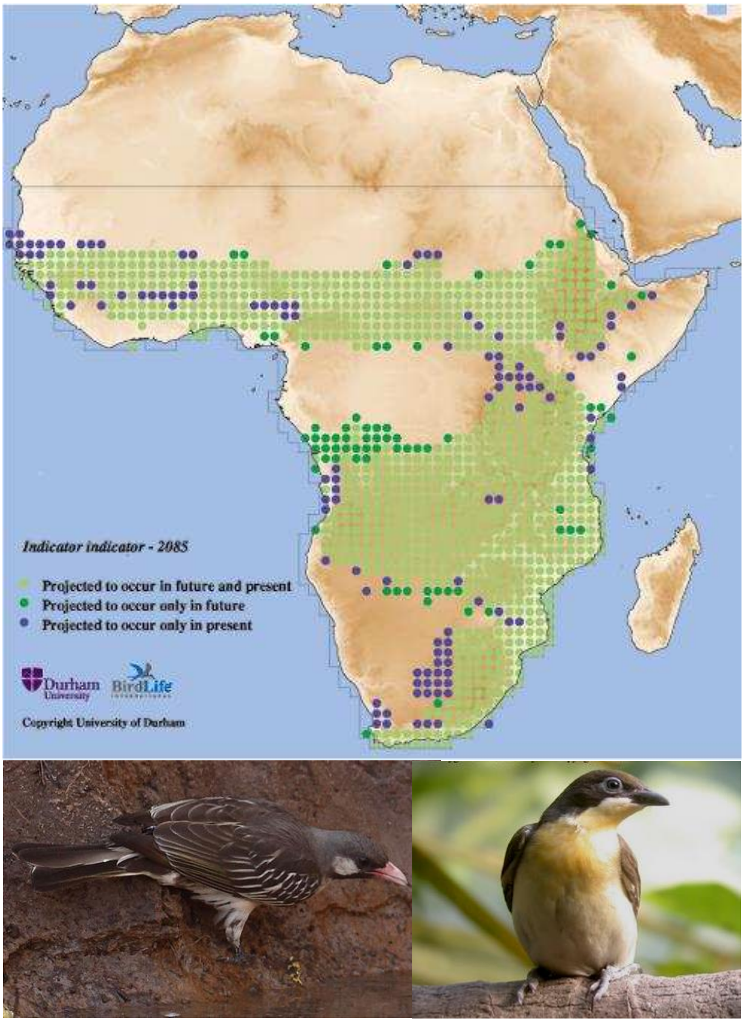


Figure 1 – Greater Honeyguide distribution and morphology. a) Birdlife International distribution map of the Greater Honeyguide, *Indicator indicator*, in 2011 and that projected in 2085; **b)** *I.indicator* in brown-grey adult plumage; **c)** *I.indicator* in yellow-breasted juvenile plumage.

Image sources:

a) http://www.birdlife.org/datazone/speciesfactsheet.php

b) http://www.flickr.com/photos/peetvs/3724484198/

c) http://blog.dareneiri.com/category/general/

All retrieved 18/4/2011.

From the above description it can be seen that communication by *I.indicator* to its human foraging partner is active, directed, and event-precipitated (commencing upon beholding a potential human recruit). That the mutualism is a temporary one, in that it exists for a discrete period of time for the purposes of gaining food, potentially adds a layer of complexity over constant, obligate mutualisms, since an element of 'initiative' on the part of the bird must be present in order to instigate mutualistic behaviour with a foraging partner. As an attempt at initiating guiding does not always occur upon *I.indicator* seeing a human, likely as a result of low motivational state associated with territorial display pre-occupation or lack of hunger, several conditions must be cognitively assessed as being met (e.g. potential recruit present + hunger state + territorial display currently not a priority) before the sight of a human will elicit a guiding attempt by the bird. Guiding also requires the guide to physically accompany a recruit to an object that is not itself nor the recruit but a third object (the food source), an ability that necessitates further cognitive sophistication in being able to memorise a location relative to a current position and lure a target recruit towards it.

In line with the apparent complexity and dynamism of this type of behaviour, few other comparable examples exist in the literature. Recent research on reef-dwelling groupers in Egypt's Red Sea presents evidence that a few species of the *Plectropomus, Gymnothorax* and *Siderea* genera (Andrea Bshary – pers. Comm 2011) initiate joint hunting with sympatric moray eels, and, with behaviour strikingly similar to *I.indicator's* guiding, even lead them to the location of concealed prey that the groupers cannot flush out themselves, the location of which is communicated from grouper to moray via characteristic head shake displays (Bshary *et al* 2006). Anecdotal reports suggest possible leading behaviour directed at humans and other predators by ravens, *Corvus corax*, as an exploitation of these predators' superior ability to open tough-hided carcasses (Bernd Heinrich – pers.comm. 2011); this observation is yet to receive scientific substantitation, however. Tandem-running in ants (e.g. Wilson 1959) has similarities to guiding in terms of the use of communication (tactile and chemical) to stimulate change in locomotive behaviour of a partner (following), but so far it has only been formally observed between conspecifics – though it is conceivable that the behaviour may yet be discovered in commensal or socially parasitic ants and their so-called 'slaves' (e.g. Diehl, Junqueira & Berti-Filho 2005; Achenbach & Foitzik 2009). Similarly, the active, directed, locomotive behaviour-changing phenomenon of the honeybee waggle-dance has not encountered the same evolutionary challenge of overcoming interspecific boundaries of communication, though it has had the arguably even larger challenge of reaching an evolutionary stage in which semantic meaning is encoded into the display (von Frisch 1967). A final possible example of guiding-related behaviour involving active, directed communication is that occurring between a shepherd and his sheepdog when working a flock. However, this partnership cannot necessarily be defined as mutualistic, since the degree of uniquely-obtained benefits that accrue to both parties has not been elucidated; the relationship also has features, such as a drive for social contact, which may identify it better with intraspecific-type cooperative behaviour than interspecific mutualism (see McConnell & Baylis 1985 for discussion of sheepdog behaviour).

It is worth noting that some anecdotal evidence suggests that mammals other than humans and some honeyguides other than *I.indicator* may also be involved in honey-hunting mutualisms, therefore increasing the number of interspecific guiding relationships known. However, as will be discussed later, unequivocal evidence of guiding by honeyguides is available for humans and *I.indicator* as the foraging partners alone. The guiding behaviour of *I.indicator* is, then, one of only two cases (the other being guiding by groupers) in the primary literature to date of mutualistic guiding – the stimulation of recipient locomotive behaviour towards a target location by a heterospecific signaller using active, directed communication, leading to an outcome beneficial to both parties. The importance of its study thus becomes clear, especially in light of the increasing interest in interspecific communication: the winter 2010 meeting of the Association for the Study of Animal Behaviour (ASAB) was in fact entirely devoted to the subject. Furthermore, conspecific cooperation during hunting by common chimpanzee groups has been regarded by primate researchers Christophe and Hedwige Boesch as being difficult for animals outside the higher primates to achieve. In their report on group hunting by the Taï forest group, they conclude that "Some abilities of the higher primates may be necessary for cooperation...." and that "...Taï chimpanzees hunt in the most elaborate way known for animal hunters." (Boesch & Boesch 1989). While one or both of these statements may be true, this interpretation also raises the possibility that, in light of the existence of potentially-complex mutualistic foraging (guiding) by honeyguides and groupers, behaviourists may be in danger of either i) overestimating the complexity of cooperative and mutualistic (interspecifically cooperative) behaviours, or ii) underestimating the number of taxa capable of cooperative/mutualistic behaviours that are genuinely as complex as they appear.

A key difference between the cooperation seen in the Taï chimps and the mutualistic behaviour seen between *I.indicator* and humans could be the ability to switch between roles within hunting and foraging events. Chimps are able to alter their role during a hunt in response to a changing situation, switching between acting as chaser, blocker, beater etc. as and when required (Boesch & Boesch 1989). *I.indicator's* role in guiding is much more fixed, with it invariably assuming the position of guide. Nevertheless, observations of guiding report a degree of variation within the guiding 'holotype' that could imply some level of plasticity to the behaviour.

Despite the importance of guiding to our understanding of cooperative and mutualistic behaviours, however, it is much under-represented in the primary literature, and not always well-known even amongst researchers of interspecific behaviour (straw poll of attendees of the ASAB 2010 winter meeting on interspecific communication).

Dedicating more research hours to guiding's intricacies could help place it and other interspecific behaviours in context of complexity, and allow more informed assessment of the abilities of organisms, such as the higher primates, traditionally regarded as having superior capacity in these areas.

However, at a time when the importance of interspecific behaviours is finally beginning to be fully appreciated, there are rising concerns that the honeyguide-human partnership could be on its way out due to certain socio-economic changes occurring across Africa (Friedmann 1955; Isack 1987; Dean, Siegfried & MacDonald 1990; Short & Horne 2001). This possible decline is not only of concern to evolutionists, ecologists and neuroscientists wishing to study the behaviour, but is also a potential conservation issue if *I.indicator* is at all reliant on the nutritional end-goal of guiding: honeycomb.

It is therefore with some urgency of purpose that I present here the results of a comprehensive literature analysis on honeyguides and guiding, with the **aims** of producing:

i) a **literature analysis** evaluating the degree of, and reasons for, scant presence of the subject in primary literature available to researchers, with focus on the accessibility and exposure of honeyguide literature to the scientific community in general.

ii) a **synthesis of the main findings** of the fraction of that literature concerned with *I.indicator*'s guiding in order to collate past and current directions of its research into one work whilst also exposing less accessible primary and secondary literature to the wider scientific community.

iii) a collection of **future research directions** recommendations arising from that synthesis to identify the primary gaps in our knowledge of guiding by *I.indicator*, with the hope of encouraging upcoming researchers into study of an important behaviour that may, due to low exposure, be otherwise unknown to them.

Literature Analysis

Background

The association between *Homo sapiens* and *I.indicator* has likely existed for thousands of years (Friedmann 1955) with knowledge of the partnership accordingly existing in African tribal legends passed on by word of mouth, generation to generation (for examples see Blench 2008; Shropshire 1931; Smith 2011; Isack 1987). However, written knowledge of honeyguides begins in the 3rd century AD, with Chinese writers briefly recording information on the African wax eating birds, passed on by their correspondents in the region (Short & Horne 2001). The next known mention of honeyguides is in a book, written in 1569 and printed in 1609, named 'Ethiopia Oriental'. Its author, the Portuguese missionary João dos Santos, talks of "sazu passaro que come cera", a bird that eats wax – 'sazu' being the local native name for both *I.indicator* and the smaller *I.minor* – feeding on his beeswax altar candles (Friedmann 1955). Over the following two centuries, *I.indicator* infrequently crops up in text in the travelogues of missionaries and explorers (see Friedman 1955 for details), until in 1777 it is formally described by Andrew Sparrman (Friedmann 1955). However, although his account makes reference (as others had done so before him) to the birds' guiding behaviour, it is not until 1951 that the first detailed and 'scientific' record of guiding appears (Skead 1951). Early academic journal pieces (the earliest I recovered being that of Leadbeater, 1833) describe guiding in a vaguer and more haphazard way, but nevertheless mark the onset of guiding and honeyguide biology being set down in a way semi-accessible to the scientific community. The letters and personal journal entries making up the body of honeyguide references preceding Leadbeater's 1833 article in *Transactions of the Linnean Society of London* are, sadly, lost to the average researcher now, since they reside in personal collections or in small, specialist libraries. I have, therefore, been unable to include them in this literature analysis, being as they are effectively inaccessible to the world at large. The timeline of references, then, begins with that 1833 one of Leadbeater's and runs until the time of writing – early 2011. Also of interest, though not precisely relevant to a review of the scholarly literature, are the depictions of honeyguides appearing in the popular media. As such, these are not included in the literature review, but are detailed in appendix 1 for interest.

Methods

I have attempted to recover all scholarly literature – both journal items and books – making reference to any member of the honeyguide family as a main topic. I have then graded the resulting items into three classes of relevance to guiding by *I.indicator*: 'all honeyguides' – those items discussing any member of the honeyguide family (ie. all items retrieved for analysis); *I.indicator* – those items with *I.indicator* as a main subject (ie. a fraction of the 'all honeyguides' class); and 'guiding' – those items with *I.indicator*'s guiding as the primary focus (ie. a fraction of the '*I.indicator*' class).

Items were recovered using a variety of methods (entering honeyguide-related search-terms in scholarly search engines and journal homepage search fields, searching through the reference lists of honeyguide books and journal articles, looking through paper copies of defunct African journals I was lucky enough to have access to, corresponding with over thirty African ornithologists to obtain leads on less accessible items) and the ease of doing so recorded for later ratings of accessibility to the average researcher. This 'accessibility rating', governed by meeting or falling short of the criteria detailed in box 1, is separate from, and subtly different to, the two additional measures of 'exposure' I include (journal's 5-year impact factor and the number of times the item is cited by others), although an additional measure of exposure (presence or absence of an item's citation on Google Scholar) is used in calculating the accessibility rating (again, see box 1 for details). 'Exposure' is included as a measure for the reason that, although usually concordant with accessibility (compare charts 1-3 with charts 4-9), items will occasionally have a high exposure (such as being in a premier journal and being much-cited) but be of slightly lower accessibility to the average scientific reader by dint of requiring journal membership for access; the reverse may also be true, with low exposure items, possibly in small, regional African journals with restricted readership, being unexpectedly easy to access if one knows about the item's existence. This is thanks to the rise of charitable organisations scanning, and making available free in online databases, issues of old, defunct journals – the Biodiversity Heritage Library (http://www.biodiversitylibrary.org) is one such organisation. The best ways of accessing all the journals that items have been recovered from in this literature analysis are listed in appendix 2. The existence of free membership to certain journals (e.g. *Ibis*) for institutions in the developing world, through the OARE (Online Access to Research in the Environment) scheme, is not considered in this analysis, since it is difficult to draw broad conclusions about accessibility from such patchy and changeable membership concessions.

Box 1 – derivation of the 'accessibility rating'.

Since the focus of this literature analysis is to evaluate the degree to which literature on honeyguides has entered, or has the potential to enter, the general scientific consciousness, any measure of accessibility must for these purposes take account of not only the ease of accessing a piece of literature once it is already known about, but also the likelihood of any researcher being made aware of it in the first place.

Currently, the commonest method of searching the scholarly literature is to enter search terms in a computer-based scholarly search engine, either a general one such as Web of Science, or a journal's own search engine on the journal homepage. I have therefore incorporated the presence or absence of an item's citation on the scholarly search engine 'Google Scholar' with the subsequent ease of the item's access (its basic accessibility), in order to produce a compound measure of exposure likelihood to a researcher and likelihood of that researcher then being able to view the full item. I chose to keep the 'presence/absence on Google Scholar' measure of exposure separate to the two additional measures of exposure ('5-year journal impact factor' and 'number of times cited by others') for the reason that the latter two are less relevant to an active search process by a researcher interested in the broad field of interspecific behaviour, and more relevant to a potentially interested researcher happening across them passively – two significantly different processes by which the honeyguide literature could be encountered.

The accessibility rating, then, is a categorical one based on the two criteria discussed – presence/absence on Google Scholar plus ease of subsequent access to the whole item – producing a five-rank system:

5: listed on Google Scholar (GS) and available free online.

4: listed on GS and available online through journal for a fee or as new copy if a book.

3: listed on GS and available through journal as printed copy back-issue or as secondhand copy if a book.

2: not listed on GS and available through journal as printed back-issue or scanned-copy databases online.

1: not listed on GS and effectively unavailable.

Google Scholar was the scholarly search engine of choice for the reason that it returned the greatest number of results in response to honeyguide-related search terms when compared with other (even subscription-based) scholarly search engines (e.g. the search term 'honeyguide' returned 9 relevant results in the free-access Google Scholar, compared with only 5 in Web of Knowledge and 4 in Scopus, both of which are subscription-based services, and 2 in the free-access Wiley Online Library, which returns results from Wiley-published journals alone). This is partly due to date limitations on the items held in these other search engine databases (1945 is the earliest held scientific item in Web of Knowledge, for instance – Jacsó 2004). The use of Google Scholar thus produces a 'best case' or 'conservative' scenario for search results on honeyguide literature. Additionally, Google Scholar no longer suffers from the problem it has previously been criticised for (Jacsó 2005) of not having access to the large body of journals owned by Elsevier.

Nb: Basic accessibility, uncompounded with Google Scholar exposure, is recorded separately for interest in **appendix 2**.

In order to convert these attributes of interest – accessibility and exposure – into handleable data, all items recovered are tabulated in a Microsoft Access database with the following fields: journal name (if applicable), year of publication (to enable analysis of peaks and troughs in levels of research across the centuries), journal's 5-year impact factor with year ending 2007 (5-year is a more long-term estimate of a journal's readership and exposure level than is a yearly impact factor, and year ending 2007 was chosen as the only readily accessible year available through Thomson Reuters Impact Factor – though this doesn't compromise the aims of the analysis in any case, since a picture of availability and exposure to today's, rather than past, researchers is the intended outcome), number of times the item has been cited by others (as an additional measure of exposure), accessibility rating (based on the criteria detailed in **box 1**), and whether the item was concerned with honeyguides in general, *I.indicator*, or *I.indicator*'s guiding. A field for the item's full citation beginning with author name was also included.

The data from these fields, excepting journal name and full citation, were then converted into three distinct sets of charts, all with year of item publication on the x axis, each consecutive five-year period making up a data class for clarity of viewing, and number of publications in that five-year period on the y axis. The plot itself was a stacked bar chart, the stacking being colour-graded by the particular focal data trait – accessibility rating, 5-year journal impact factor or 'cited by' (number of times item is cited by other literature) – to compose the three chart types. Within each chart type the data were further sub-divided into three charts: one showing a plot across time of *all* honeyguide-related items, one showing the fraction of those concerned with only *I.indicator*, and one showing the fraction focusing on *I.indicator*'s guiding. This produced a set of nine charts, the raw data for which can be seen in **appendix 3**.

Results

120 items with honeyguides as a main subject were retrieved, spanning the years 1833-2010. Of these, 56 were concerned with the Greater Honeyguide (*Indicator indicator*) as a main subject; the rest concerned other members of the family Indicatoridae or focused on the general taxonomy or biology of the whole family. Of the 56 items regarding *I.indicator*, only 16 focused in detail on its guiding behaviour; 5 of these items, constituting both books and journal articles (Skead 1951; Friedmann 1955; Isack 1987; Isack & Reyer 1989; Short & Horne 1990) contained original observations of guiding conducted in a methodical and 'empirical' manner. The rest were either editorial or review articles (N=5) or were anecdotal-style observations recorded as field notes by amateur naturalists and then sent in to small, regional journals as 'interest pieces' (N=6).

The distribution of items across the 179 years of retrievable literature shows a 'background' publication rate from 1833 to present (2011) of never more than 4 items per five-year period, with a fifty-three year long peak from 1950 to 2004 within which every five-year period bar two (1960-64, N=2; 1995-99, N=4) exceeds 4 publications. More than half of the five-year periods in this peak (6/11 = 55%) exceed 6 publications, with the greatest number of publications being in 1985-89 (N=14). Of some concern is the fact that this peak in publications falls off before the present day, indicating from the relatively small dataset present here that interest in honeyguides as a research topic is waning (though this could be a stochastic fluctuation which will be quickly succeeded by years of greater publication volume). Additionally, further analysis reveals that only two sets of authors (Friedmann and Short & Horne) are responsible for 30% of the literature published in that fifty-three year peak (number of publications by those authors being N=15 and N=12, respectively) while the remaining 62 items are authored by fifty-one different author sets, each of which never exceed 3 publications within the peak (see **chart 10**).

The accessibility of items was generally low (see **charts 1-3**), with 73/120 (60%) of items in the 'all honeyguide literature' class falling into the lowest two ranks of the five-rank accessibility rating and 85/121 (70%) falling into rank 3 or below (**chart 1**). This means that 70% of honeyguide literature is not available in electronic copy unless it is fortunate enough to have been scanned into a specialist database by a charitable organisation, in which case it rarely appears as a citation on a scholarly search engine and is thus unlikely to be encountered by a prospective researcher. The accessibility distribution for the literature concerned with *I.indicator* alone is similar (41/56 = 73% of items fall into rank 3 accessibility or lower – see **chart 2**), as is that of the literature concerned with only guiding (11/16 = 69% of items fall into rank 3 accessibility or lower – see **chart 3**).

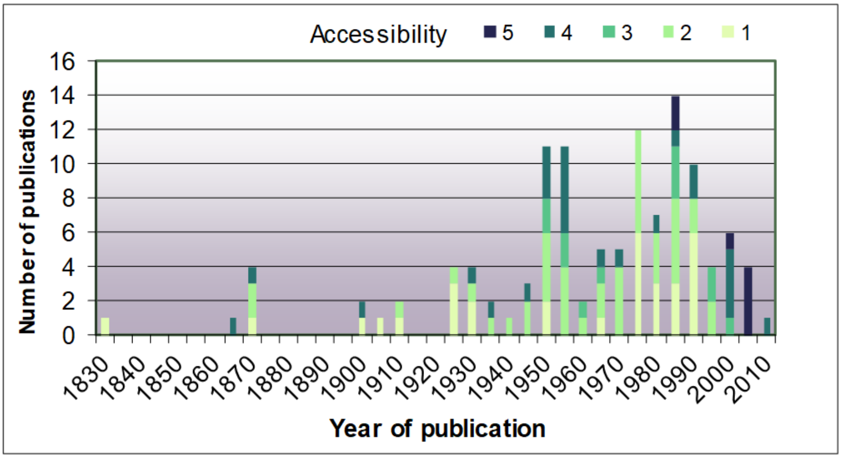


Chart 1 – All scholarly publications with any member of the honeyguide family, Indicatoridae, as a main subject, ranked by accessibility to the general scientific community.

Key to rankings: 5: listed on Google Scholar and available free online, 4: listed on Google Scholar and available online through journal for a fee or as new copy if a book, 3: listed on Google Scholar and available through journal as printed copy back-issue or as second hand copy if a book, 2: not listed on Google Scholar and available through journal as printed copy back-issue or specialist scanned-copy databases online, 1: not listed on Google Scholar and effectively unavailable.

Nb: Jubb 1966 (*Bokmakierie*), Louette 1981 (*Revue Zoologie de Afrique*), MacDonald 1994 (*Africa – Environment & Wildlife*), and Landrey 1925 (*Blythswood Review*) are listed on Google Scholar but are unavailable as these journals are defunct, so articles are categorized as accessibility 1.

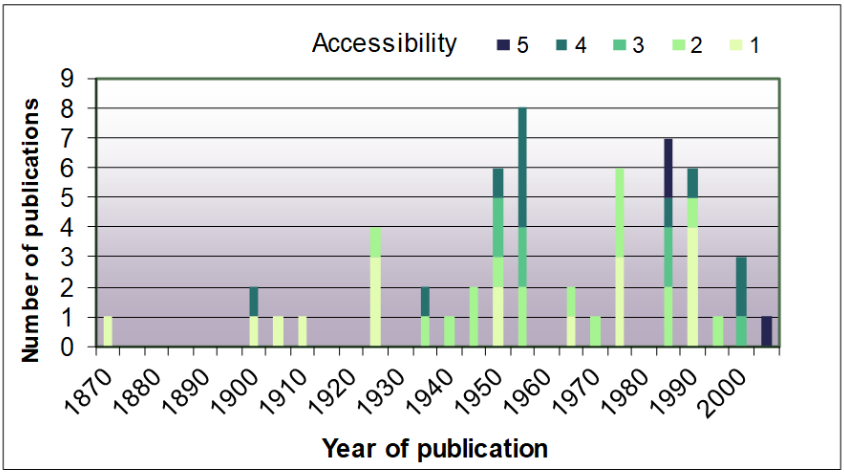


Chart 2 – All scholarly publications with the Greater Honeyguide, *Indicator indicator*, as a main subject, ranked by accessibility to the general scientific community.

Key to rankings: 5: listed on Google Scholar and available free online, 4: listed on Google Scholar and available online through journal for a fee or as new copy if a book, 3: listed on Google Scholar and available through journal as printed copy back-issue or as second hand copy if a book, 2: not listed on Google Scholar and available through journal as printed copy back-issue or specialist scanned-copy databases online, 1: not listed on Google Scholar and effectively unavailable.

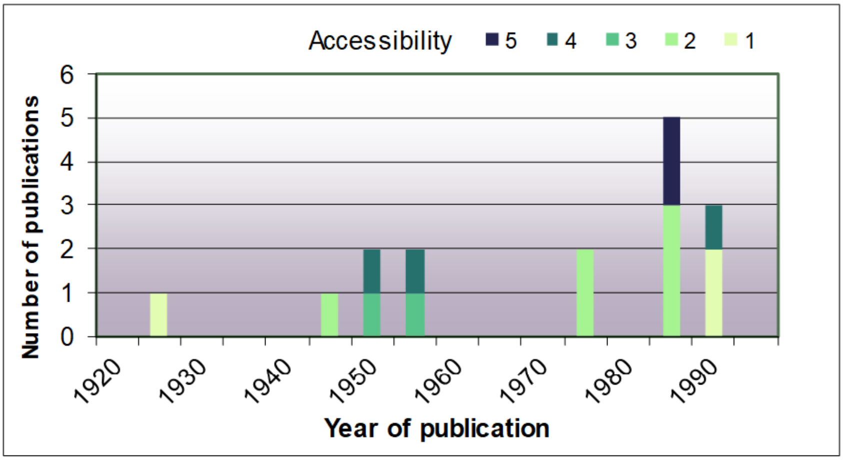


Chart 3 – All scholarly publications with the Greater Honeyguide's (*Indicator indicator*) guiding behaviour as a main subject, ranked by accessibility to the general scientific community.

Key to rankings: 5: listed on Google Scholar and available free online, 4: listed on Google Scholar and available online through journal for a fee or as new copy if a book, 3: listed on Google Scholar and available through journal as printed copy back-issue or as second hand copy if a book, 2: not listed on Google Scholar and available through journal as printed copy back-issue or specialist scanned-copy databases online, 1: not listed on Google Scholar and effectively unavailable.

The number of times an item was cited (a measure of the item's exposure to the scientific community) also tended to be low, with 103/120 (85%) of all honeyguide literature being cited 10 or fewer times and 86/120 (71%) being entirely uncited (see **chart 4**). This gives a low probability of honeyguide literature being encountered by researchers during a 'passive' search process (i.e. happening across the literature while reading another article citing it), so giving little opportunity for scientific interest in honeyguides to be piqued. A similarly low proportion of the literature on *I.indicator* was cited (52/56 = 93% being cited 10 or fewer times, and 39/56 = 70% being entirely uncited – see **chart 5**), as was the literature on *I.indicator*'s guiding (11/16 = 69% being cited 10 or fewer times, and 9/16 = 56% being entirely uncited – see **chart 6**).

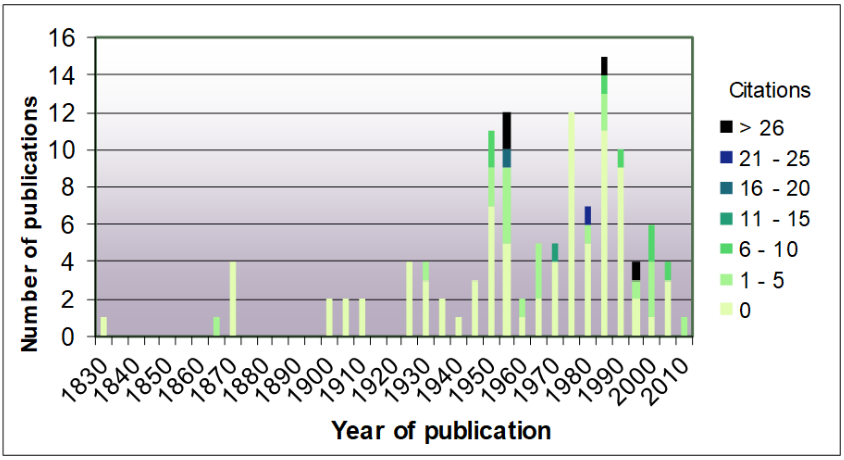


Chart 4 – All scholarly publications with any member of the honeyguide family, Indicatoridae, as a main subject, ranked by number of times the item has been cited by other literature according to Google Scholar.

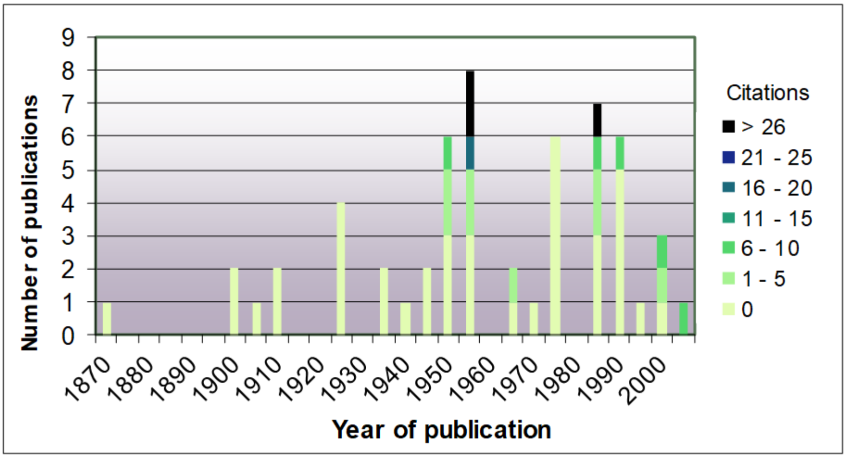


Chart 5 – All scholarly publications with the Greater Honeyguide, *Indicator indicator*, as a main subject, ranked by number of times the item has been cited by other literature according to Google Scholar.

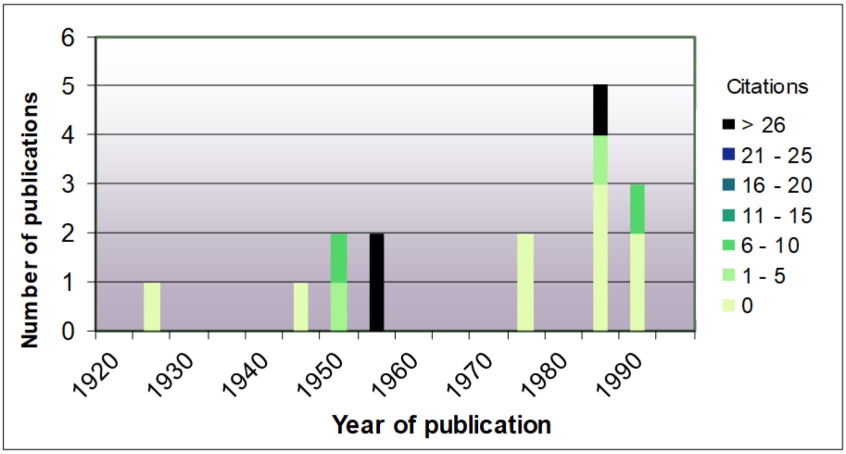


Chart 6 – All scholarly publications with the Greater Honeyguide's (*Indicator indicator*) guiding behaviour as a main subject, ranked by number of times the item has been cited by other literature according to Google Scholar.

The exposure measure of 5-year journal impact factor (acquired from Thomson Reuters Journal Impact Factor database) of the journal the item appears in (if the item is not a book or symposium report) was low given the rarely-approached upper limit of just over 30.00. Although, like the previous two measures (accessibility and number of times cited), it is impossible without further inter-subject comparative research to give a relative context to these results (it may be that an 'average' subject's literature is also largely inaccessible, uncited and of low journal impact factor), nevertheless an absolute statement can be tentatively made: that the likelihood of a researcher not already familiar with the honeyguide literature encountering an item in this analysis is low at present. For further points on relative measure limitations, see the Literature Analysis discussion.

5-year journal impact factors for all honeyguide literature, then, were low within the possible scale, with 96/105 (91%) of journal articles being published in a journal of only 5-year impact factor 2.00 or less, and 63/105 (60%) being published in a journal with no impact factor allocated (**chart 7**). For the fraction of that literature concerned with *I.indicator*, 39/47 (83%) appears in journals of 5-year impact factor 2.00 or less, and 24/47 (51%) appears in journals with no impact factor (**chart 8**), values which are marginally better than for the honeyguide literature in general. For the fraction of the literature regarding only *I.indicator*'s guiding, 8/13 (62%) appears in journals of 5-year impact factor 2.00 or less, and 5/13 (38%) appears in journals of no impact factor (**chart 9**) – a further improvement on the high proportion of general honeyguide literature found in low-impact journals.

An additional analysis was made of the correlation between number of times a piece of general honeyguide literature was cited and the 5-year impact factor of the journal it appears in. A roughly linear relationship between these two attributes can be expected, since a journal's impact factor is partially reliant on the citation numbers of its articles. Accordingly, **chart 11** shows a general trend of increasing 5-year journal impact factor with increasing citation number of the focal paper, thus the relationship expectation holds true for the honeyguide literature retrieved, excepting two outlying review articles which appear in high impact factor journals, but for which researchers citing the subject matter would simply cite the original work the article reviews.

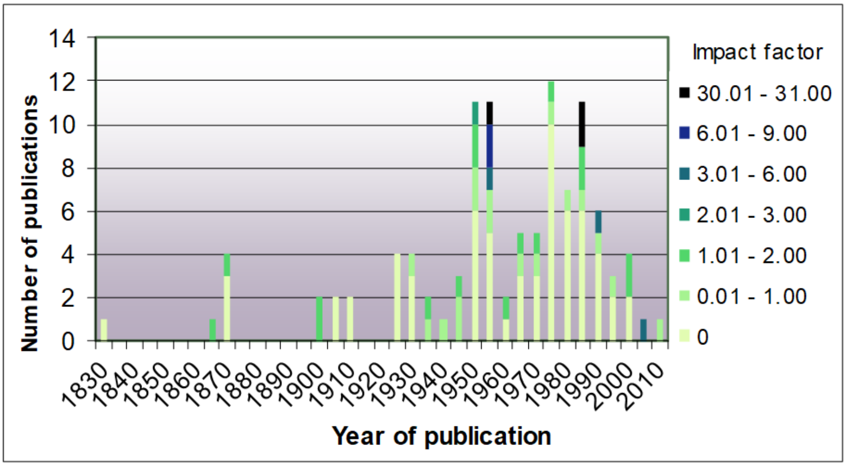


Chart 7 – All scholarly publications with any member of the honeyguide family, Indicatoridae, as a main subject, ranked by 5-year impact factor (year ending 2007, acquired from Thomson Reuters Journal Impact Factor database) of the journal they appear in, if applicable.

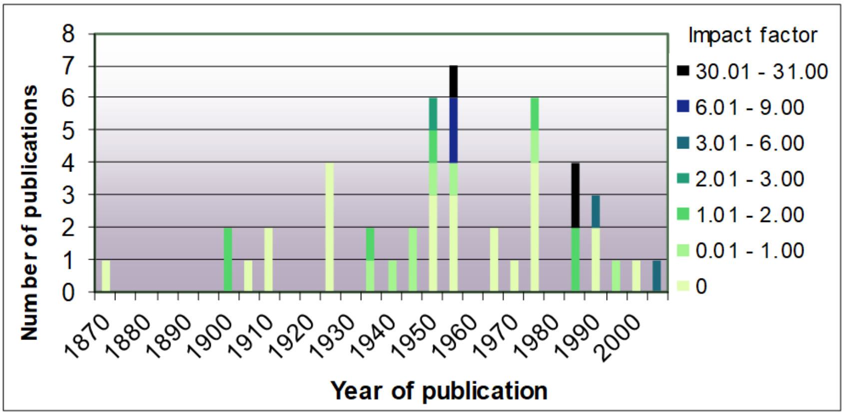


Chart 8 – All scholarly publications with the Greater Honeyguide, *Indicator indicator*, as a main subject, ranked by 5-year impact factor (year ending 2007, acquired from Thomson Reuters Journal Impact Factor database) of the journal they appear in, if applicable.

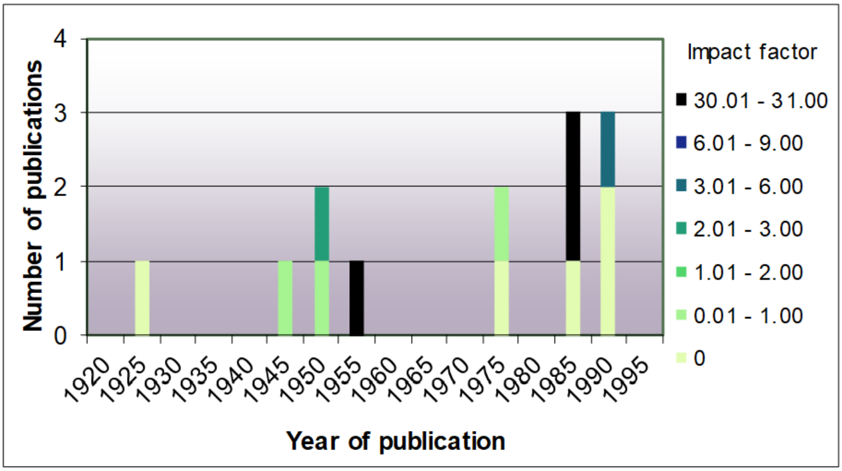


Chart 9 – All scholarly publications with the Greater Honeyguide's (*Indicator indicator*) guiding behaviour as a main subject, ranked by 5-year impact factor (year ending 2007, acquired from Thomson Reuters Journal Impact Factor database) of the journal they appear in, if applicable.

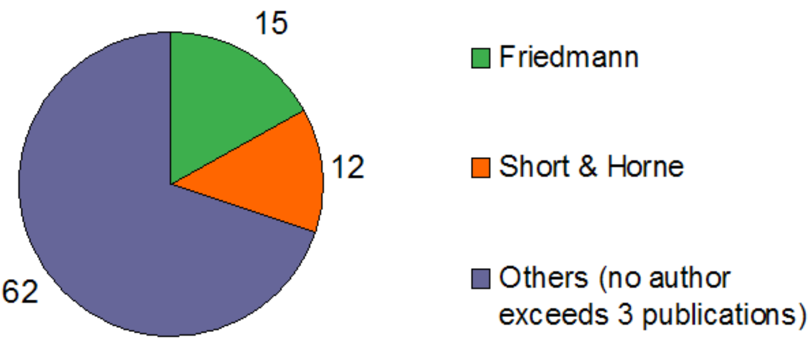


Chart 10 – The proportions of general honeyguide publications attributable to which authors, from within the peak of publishing occurring 1950-2004.

The peak in publications is defined as the marked increase in publications, 1950-2004, above the 'background rate' of 4 or fewer publications per five-year period outside this peak.

Two sets of authors alone (Friedmann and Short & Horne) account for 30% of publications in the 1950-2004 period, making this peak attributable in large part to their research activities, and less strongly attributable to a generalised increase in honeyguide research interests.

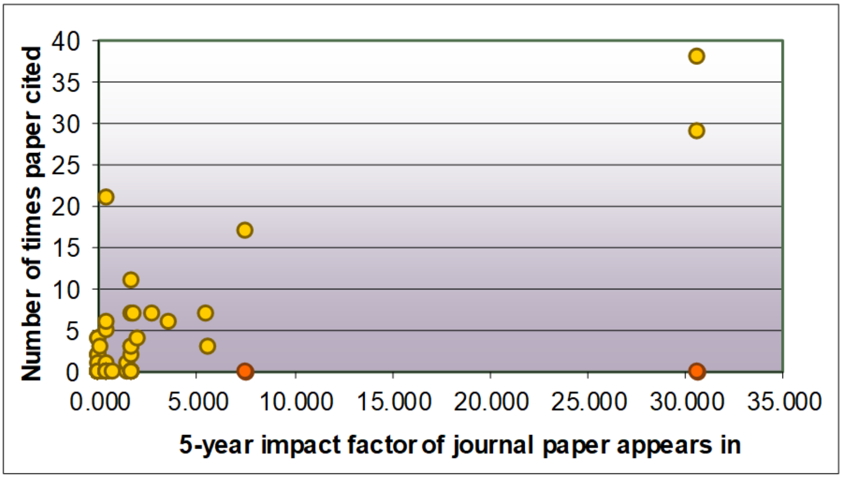


Chart 11 – The number of times papers in the general honeyguide literature have been cited plotted against the 5-year impact factor of the journal each paper appears in.

The two outliers highlighted in dark orange are review articles which, accordingly, have low citation numbers but appear in high impact factor mainstream journals (*Quarterly Review of Biology* at a 5-year impact factor of 7.476, and *Nature* at a 5-year impact factor of 30.616).

Discussion

The results of the literature analysis demonstrate that the majority of general honeyguide literature is of low accessibility (70% is unavailable in electronic form excepting occasional coverage by scanned databases created by charitable organisations), not well-cited (71% is not cited at all) and does not appear in high impact factor journals (91% appears in journal with a 5-year impact factor of 2.00 or less and 60% appears in journals with no impact factor) (see **charts 1**, **4** and **7**). Across the fraction of the literature concerned with I.indicator and I.indicator's guiding (**charts 2**, **3**, **5**, **6**, **8** and **9**) a similar picture materialises (though these two sub-topics fare a little better than the general literature when it comes to the impact factor of journals they appear in, occurring only 51% and 38% of the time, respectively, in journals with no impact factor). This leaves little opportunity for researchers potentially interested in the area of interspecific behaviour to encounter this large body of often informative, but more frequently question-posing, literature.

It is worth noting that the majority of published items are 'anecdotal'-style field notes sent in to local African journals (or to authors collecting research material for books, e.g. Friedmann 1955) by amateur naturalists, making them both tantalisingly informal in their observations, but also particularly hard to access and of low-exposure; they would in fact, only be encountered by researchers already interested in the ornithology of the journal's geographical region of coverage – not necessarily a background which confers scholarly expertise in evolution and behaviour. The only three items of the honeyguide literature to have appeared in the two most prestigious journals, Science and Nature, are a short (anonymous) editorial on Friedmann's 1955 'The Honeyguides' appearing in Science in 1956, Isack & Reyer's 1989 report of their original research into I.indicator's guiding sessions in Kenya (appearing in Science), and a short Nature News & Views piece by Robert May appearing soon after, reviewing the Isack & Reyer work. Appearing in these two high-profile, high-circulation, broad subject-base publications does allow I.indicator's guiding habits some brief high exposure to scientists coming to interspecific behaviours from a non-(African)ornithological background. However, because the current body of research raises just as many questions as it answers in terms of guiding behaviour's evolution, ontogeny and stability, and because a 1950-2004 peak in research indicates a decline in honeyguide research interest in the most recent years, the subject could certainly do with being reintroduced to the general scientific consciousness.

In terms of the distribution of literature types, five modes of publication were identified (see **appendix 3** for individual items' format): journal articles (review, original observations or original experiments), books (including field guides devoting a greater than usual amount of text to the biology and behaviours of honeyguides but excluding those numerous volumes with basic field identification notes alone), symposium reports, doctoral theses and expert-authored web-based documents. Of these, symposium reports are commonly the most difficult to obtain, an element of luck being required in their long-term preservation, as are theses for the reason that it is entirely up to the awarding institution whether they release the manuscript for interlibrary loan or up to author discretion in the case of making a web-based electronic copy available. Six articles in symposium reports (all ornithological in nature) were recovered and two doctoral theses, Hussein Isack's 1987 Oxford University one and Colleen Begg's 2006 University of Pretoria one on honey badgers, Mellivora capensis, (with a large section on the mammal's proposed mutualism with I.indicator). The latter is available through the University of Pretoria's Electronic Theses and Dissertations Service but the former has no copy in either electronic or photocopied form and thus Oxford is understandably conservative in lending it. Journal articles make up the bulk of the honeyguide literature (105 of 121 items) and are extremely variable in their ease of obtainment, as has already been discussed, but those which are at the lower end of the accessibility spectrum are virtually impossible to acquire as anything beyond a citation (containing a honeyguide-related word in the title) in another item. Indeed, considering the number of honeyguide-related items per issue of the defunct East African Natural History Society Bulletin (very roughly one item per three issues), there are likely more honeyguide articles in existence in this journal than the two have I retrieved from the fortunate access I had to a partial run of the publication through a private collector. This journal, usually only patchily available in small local (East and South African) libraries, is likely not the only publication with such a restricted modern availability, though it appears to be the worst-affected of the journals I have come across. Books are, on the whole, easier to obtain than most journal items, though they are rarely available through libraries (due to the specialist nature of the subject matter) so must be purchased. Six books were recovered with honeyguides as a main or specially-treated subject, four of which are by Short & Horne and are easily purchased new or second hand (though often for a £50-£70 price tag); of the other two, Johnsgard's 'Avian Brood

Parasites' is still available new as the 1998 edition (again, for £50-£70) whereas Herbert Friedmann's excellent and exhaustive 1955 monograph 'The Honeyguides' is out of print and difficult to obtain in hard-copy but is available unabridged as a scanned copy from the information donation based organisation Internet Archive (http://www.archive.org/stream/bulletinunitedst2081955unit/bulletinunitedst2081955unit_djvu.txt). Turning finally to expert-authored web-based documents, two were recovered (Lowther 2007; Blench 2008), both easily accessible to anyone with internet access searching for honeyguide-related terms in a scholarly search engine.

To return for a moment to the 1950-2004 publication peak referred to earlier, deeper examination of the peak's author composition (**chart 10)** reveals that 30% of the peak's publications are due to the research activities of just two sets of authors (Friedmann and Short & Horne). This means that there are few researchers in recent times studying honeyguides intensively, thus only a small number of researchers may be getting to know their subject thoroughly and intimately (an exception to this is Hussein Isack, who has published only two items on honeyguides yet is likely one of the world's authorities on their behaviour, having focused his aforementioned PhD for Oxford University entirely on I.indicator). It also suggests a contributing factor for the apparent fall-off in honeyguide research in recent times: neither Friedmann nor Short & Horne, responsible for the majority of book-based items on honeyguides, are currently publishing – Herbert Friedmann and Jennifer Horne being deceased (Rothstein, Schreiber & Howell 1988; Howell 2009) and Lester Short having exited academic life – causing a decrease in literature simply from the absence of these two author sets. The acquisition of knowledge about the honeyguides thus seems tenuously dependent in the main upon the special interests of a small handful of researchers, now no longer active, with this decrease in expertise occurring at a time when the window of opportunity for study may be closing, if concerns over the behaviour's demise prove true.

As to why the literature is scarce when it comes to material that takes a scientific approach rather than a more casual one, several things about the dissemination of information surrounding honeyguides, and particularly I.indicator's guiding, emerge as striking. The birds are constrained in distribution to areas of Africa which have not had a long written tradition of recording environmental observations; instead there has been a strong oral tradition of information transmission, evident in the wealth of spoken African legends surrounding the natural world (e.g. Shropshire 1931; Isack 1987; Blench 2008). These legends present idealised, anthropomorphic or embellished depictions of animal and plant behaviour that yet contain enough grains of truth to be perpetuated as true reflections of the way species operate and for what purposes. Thus misinformation has been propagated as truth (for instance, many naturalists over the years have been convinced by tribal legends of honeyguides purposefully leading humans to danger as vengeance for past unrewarded guiding missions – for discussion of this see Layard 1869; Landrey 1925). This 'hearsay' method of knowledge dissemination appears to affect honeyguides particularly badly, possibly because of a human need to explain the guiding behaviour that so directly impacts man's well-being meeting with the difficulties inherent in the bird's study: as Hussein Isack discovered during his PhD and others have noted, the bird lives in difficult-to-access habitat (mainly scrubby, rocky terrain full of thorny 'wait-a-bit' (Acacia genus) thicket) and is itself difficult to spot, being unobtrusively grey-brown (Isack 1987). These combined anthropogenic and ecological factors make honeyguides susceptible to both restricted and unrigorous reporting, making the outcome of this literature analysis perhaps unsurprising.

It could be argued that all the results discussed here have little meaning when not being held in comparison with the accessibility and exposure of literature on other similar subjects, since no relative measure of these attributes is thus reached. It is true that comparative studies on accessibility, citation numbers and journal impact factor would be very useful in determining whether honeyguide literature genuinely is unusually low in these categories. However, a commonsense approach would suggest that, since a significant proportion of honeyguide research has a publication date which is prior to the earliest included on many search engines (e.g. Web of Knowledge's earliest science item is dated 1945, 19% of honeyguide literature occurs before this time), it does suffer from being a lower exposure subject than subjects with more recent commencement of research. And, as mentioned in the results, the highly regional and specialist nature of the journals that most honeyguide literature appears in leads to a tentative conclusion that researchers in the general field of interspecific behaviour are unlikely to encounter research on the subject, much less have easy access to the full articles or books in each case. Add to this the scarcity of high quality empirical research already discussed, and the field of honeyguide research does begin to appear somewhat impoverished. An exhaustive list of all honeyguide literature retrieved is included in **appendix 3** as an attempt to partially remedy this, and the easiest ways of accessing each item is listed in **appendix 2** to further aid in dissemination.

Synthesis of Main Guiding Literature Findings

Cerophagy

Waxes are an unavoidable component of avian food items, constituting the cuticles of berries and insects amongst other things, but while many birds frequently consume these waxes few are able to digest them. Some birds, like the Kori Bustard (*Ardeotis kori*), are able to digest wax-like tree gums (Friedmann 1955), however true wax eating ('cerophagy') by birds able to metabolise it is known only in some seabirds (Short & Horne 2001; Isack 1987), Yellow-rumped Warblers (*Dendroica coronata*) and Tree Swallows (*Tachycineta bicolor*), both of which metabolise bayberry cuticular wax at 80-90% efficiency and less digestible beeswax (a blend of straight-chain alkanes, carboxylic acids and esterified alcohols) at 50% (Place & Stiles 1992), and honeyguides, which metabolise beeswax at between 60% (Friedmann & Kern 1956) and 90% (Downs, van Dyck & Iji 2002) efficiency. Common Bulbuls (*Pycnonotus barbatus*) and some barbets have occasionally been seen eating beeswax (Short & Horne 2001; Friedmann 1955), but their digestion of it is unknown in degree. The honeyguides' unusual ability may have originated as these other cases appear to have: by gradual increase in capacity for digesting waxes unavoidable in the diet (Isack 1987). This implies honeyguides may have begun by consuming bee larvae, although the genus *Prodotiscus* (see figure 2 for phylogeny) avoids bee products and consumes waxy scale insects instead (Friedmann 1955; Short & Horne 2001). *Prodotiscus*' non-apian diet may be derived or ancestral; it has been argued that honeyguides possess no anatomical adaptations to cerophagy, implying the diet is evolutionarily recent (Beecher 1953, in Friedmann 1955), however others argue that the birds' thick skin and membranous nostrils show anti-bee-sting adaptation and that unusually numerous fault bars in the plumage of nestlings demonstrate a nutritional reliance on waxes omitted in the diet provided by foster parents of this universally brood-parasitic taxon (Short & Horne 2001).

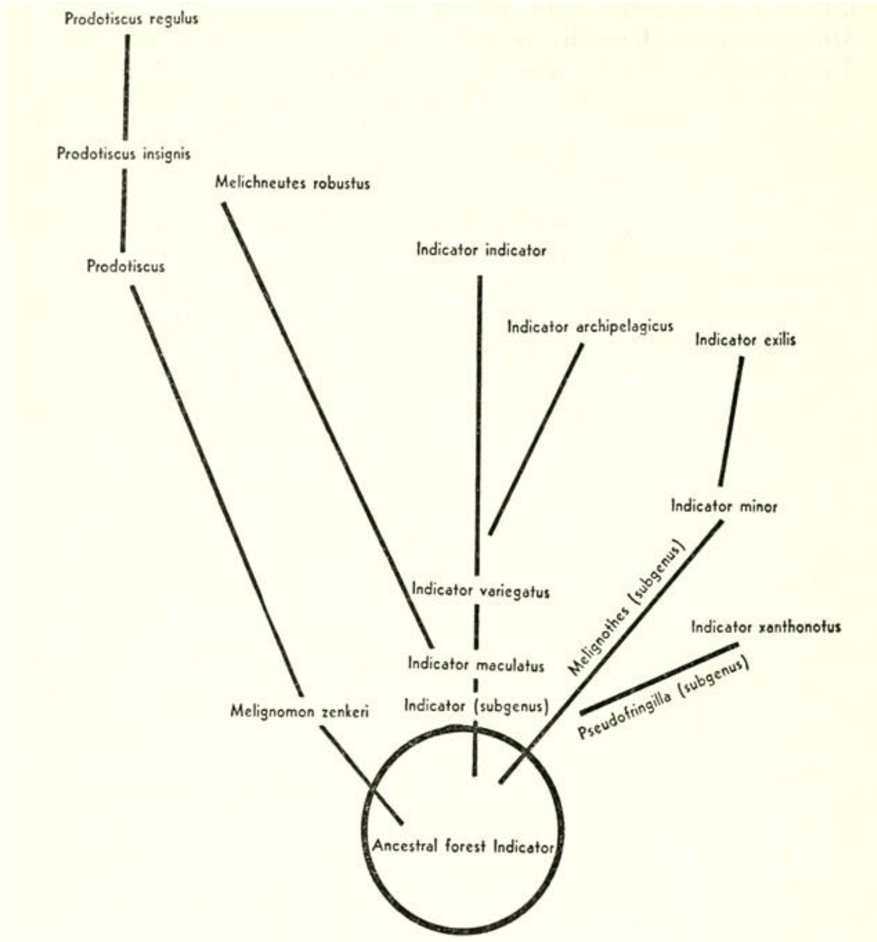


Figure 2 – Proposed phylogeny of the honeyguide family (Indicatoridae).

The ancestral forest Indicator is proposed to have arisen at a time before the African and Indian continental plates had fully separated, with the possibility of the progenitor having evolved in either continent (Friedmann 1955). *Indicator xanthonotus* and *I.archipelagicus* are the only honeyguides to have a non-African distribution, both being south Asian. Wax-eating (cerophagy) may have been the main point of divergence between the ancestral honeyguide and the mainly frugivorous barbets (Capitonidae) and toucans (Ramphastidae) and insectivorous woodpeckers (Picidae) that are the three families honeyguides (Indicatoridae) are most closely related to (Friedmann 1955).

The Friedmann 1955 phylogenetic tree that the above figure is adapted from omits six species (*Indicator pumilio, I.willcocksi, I.meliphilus, I.conirostris, Melignomon eisentrauti* and *Prodotiscus zambesiae*) for unknown reasons – although two species (*I.pumilio* and *Melignomon eisentrauti*) were discovered after Friedmann's 1955 publication. Including the six omissions, N=17 Indicatoridae species in all.

Honeyguides' wax preferences are somewhat disputed, with Friedmann's 1955 experiments finding dry, cleaned beeswax far more desirable than honeybee larvae and Isack's 1987 experiments showing comb with larval inclusions to be an equally preferable alternative; honey, however, is consistently found by both researchers to be rejected. This could be surprising given that beeswax, despite its calorie content of 38.3kJ/g (of the soft pale comb preferred to the tough dark comb with its 19.23kJ/g and two-fold handling time) (Isack 1987), is harder for most animals to extract energy from than the energetically inferior honey; however, the calorific difference is in fact seven-fold (Short & Horne 2001) which, with honeyguides' elevated wax digestion efficiency, renders the preference more understandable. The method of that improved digestion is not yet proven beyond doubt, however analysis by Diamond and Place (1988) and by Downs, van Dyck and Iji (2002) suggest it is accomplished via endogenous avian enzymes, without gross anatomical specialisation – in contrast to initial experimental outcomes by Friedmann and Kern (1956) indicating dependence upon symbiotic gut bacteria.

The degree of dependence on wax in the honeyguide diet has been well-elucidated experimentally by Ranger (in Friedmann 1955) Friedmann and Kern (1956), Isack (1987) Diamond and Place (1988) and Downs, van Dyck and Iji (2002). All researchers find honeyguides can survive on pure beeswax for 32 days – ten times longer than similar sized birds can go without sustenance, thus proving its metabolism (Kendeigh, in Friedmann 1955) – but without the usual insect element of the diet to 'dilute' the wax in the alimentary canal, the gizzard and cloaca become blocked after this point, conspiring with vitamin B_1 deficiency to cause death (Friedmann 1955). As soon as insects or bee larvae inclusions are introduced to the wax diet, though, survival is indefinite (Isack 1987), as it is on a purely insectivorous diet (Diamond & Place 1988). Wax consumption is therefore facultative in the diet rather than obligate, although Short and Horne's fault bar observation previously mentioned may suggest that a mixed insect-wax diet is ideal. The ability to utilise this under-exploited resource, which can sustain one honeyguide for 150 days per hive (Isack 1987), may confer a definite competitive advantage versus other birds (in fact cerophagy was likely a key divergence point between honeyguides and the frugivorous barbets and toucans and insectivorous woodpeckers – Friedmann 1955; Short & Horne 2001), making it likely to be more of an ecological dependence than a physiological one.

The method of honeyguides' wax detection is a far more contentious area, with olfaction proposed by Stager (1967) and Archer and Glen (1969) being only cursorily tested by them without accounting for other possible sensory detection; likewise Hepburn (2010) does not appear to exclude taste as a discriminatory mechanism. Short and Horne (2001) suggest vision and hearing are acute enough to allow hive detection, all honeyguides having a tendency to visually monitor wild hives in an area, and rigorous experiments by Isack (1987) favour this hypothesis whilst refuting olfaction, despite the unusually large olfactory tubercles present in honeyguides (Stager 1967).

Prevalence and evolution of guiding

Guiding's existence is a fascinating evolutionary puzzle ripe for investigation. As Friedmann (1955) noted, it is a behaviour unlikely to have arrived fully formed, yet is hard to imagine being useful in a partially-formed state. It is clearly not necessary to all honeyguides, since members of the family outside *I.indicator* practice cerophagy without guiding and *I.indicator* does not rely on guiding missions to source all its beeswax. Why *I.indicator* is the only honeyguide to have developed guiding is speculative only at present, but a possible combination of reasons proceed from its size (the second largest in the family at 49g – Short & Horne 2001) and habitat (relatively dry, treeless terrain that is conversely less preferred by many other honeyguide species). *I.indicator*'s large size may disallow its entrance into many wild bee hives compared to smaller sympatric honeyguides (commonly the Lesser Honeyguide *I.minor* and the Scaly-throated Honeyguide *I.variegatus*), with between 50% and 96% of nest holes estimated to be prohibitively small in Kenya, depending on local terrain (Short & Horne 2001; Isack 1987). *I.indicator* may thus require aid in breaking and entering more frequently than do its sister species, but its size also allows it competitive dominance over other Indicatoridae at opened hives (Short & Horne 2001); add to this the insect-depauperate nature of its scrubby environment, which creates more of a demand for reliance on non-insect nutriment (Short & Horne 2001), and we may have a set of circumstances favouring *I.indicator*'s unmatched utilisation of wax (Friedmann 1955) and its consequential quest for foraging help, though the direction of cause and effect here is yet to be understood. Behaviour that may be preliminary to guiding is observable in other *Indicator* spp., manifesting as their strong interest in human activity, with *I.archipelagicus*' even displaying excitement behaviour when in close proximity to people (Isack 1987), though the possibility of these behaviours being relicts of a previously present guiding propensity cannot be discounted; either way, most researchers are now agreed that, modernly, *I.indicator* alone guides, with a little room for doubt over *I.variegatus* (Friedmann 1955).

How such a behaviour began is also a speculative area. A parallel set of behaviours that could indicate the evolutionary process of guiding occurs in reef fish. Moray eels are often followed by different heterospecifics, as they stir up prey from sediment and crevices (Strand 1988). This association, which the moray appears not to benefit from, is progressed to a foraging mutualism between puddingwife wrasse (*Halichoeres radiatus*) and bar jacks (*Caranx ruber*) in which joint foraging benefits both parties' preycapture success (Baird 1993). Mutual association during foraging is further advanced in the relationship outlined in the introduction, occurring between groupers and moray eels, to arrive at a fully developed guiding behaviour (Bshary *et al* 2006). In *I.indicator*'s case, perhaps an associative learning process initially took place upon observing mammals – including hominids – raiding bees' nests and has proceeded through a similar route to reef fish, by increasing association with those mammals to gain hive leftovers and then an evolutionary move towards actively indicating hives unknown to those mammals. Feeding associations, common in fish (Ormond 1980), are also common in birds (Mönkkönen, Forsman & Helle 1996) and between birds and mammals (Dean & MacDonald 1981; Sharpe Joustra & Cherry 2010) and Friedmann (1955) notes that some of these (e.g. the European robin's attraction to soil being disturbed) can target man. Therefore guiding can be placed in a background of plentiful commensal and mutualistic behaviour of varying degrees of complexity and dependence occurring throughout various different taxa (for evolutionary reviews of the mutualism-forming process see Kostan 2002; Foster 2006).

In neither reef fish nor honeyguides is it known at which point putative associative learning becomes genetically set and heritable; this will be a task for future evolutionists and molecular ecologists. It is even suggested that guiding is not fully genetically consolidated in *I.indicator*, since it can disappear in individuals not given the opportunities to guide (discussed later), but it is hard to imagine how it could arise solely from direct or social learning in this bird which is highly solitary (Isack 1987, Short & Horne 2001; though see Friedmann 1955 p35), not raised by its own species (e.g. Spottiswoode & Colebrook-Robjent 2007) and is able to guide within a month of fledging (Short & Horne 2001). It thus seems likely that some form of learning is supported by a genetic propensity towards guiding which manifests as an innate interest in activity around hives and the animals which frequent them, and expands into the learning of something like a 'search image' (Tinbergen 1960) of these associating mammals when proximity to them is rewarded by food in an operant reinforcement process (Skinner 1966). When the 'operant' (guiding stimulus such as the presence of responsive humans) is chronically absent, such as in developed areas where people have little interest in hunting for wild honey, the behaviour may not be expressed, though whether it still remains as a genetic potential able to express upon people eliciting it, or whether it is truly lost to create a polymorphic (genetically 'guiding' and 'non-guiding') population, requires more research. There is certainly opportunity for long-term learning in these birds whose longevity is at least 10 years in the wild (Short & Horne 2001).

Two evolutionary processes which could either combine with or be alternatives to associative learning are those of mobbing and begging. A mobbing basis to guiding has occasionally been put forward by authors (e.g. Hoesch 1937; Fry 1977) linking the guiding call with a predator alarm call upon a honeyguide observing bees – a 'natural enemy' capable of inflicting damage, that inhabits precisely the resource area a honeyguide wishes to access. Mobbing, it is argued, attracts predators of a mobbing target making 'an enemy of my enemy' a desirable presence. Correspondingly, the danger inherent in exploiting 'Africanised' Western Honeybees (*Apis mellifera*) as the African honeyguides do is certainly great, with birds occasionally being found stung to death in enclosed bees' nests (Isack 1987; Short & Horne 2001) – though the wax-producing bees present before 1 million years ago would have been the stingless sweat bees (*Trigona* spp.), which honeyguides still occasionally prey upon the hives of, rather than the then Middle East-confined *Apis mellifera* (Short & Horne 2001). This makes mobbing a likely origin only if guiding arose post-lower Pleistocene, 2.6–5.3 million years after the probable Pliocene radiation of *Indicator* (Lönnberg 1929, in Friedmann 1955). Refuting the idea of mobbing, and supporting the concept of begging, is the fact that captive honeyguides begin to give guiding-like calls if starved, even though they are not in the vicinity of bees (Isack 1987). Begging calls of *I.indicator* nestlings are indeed similar to guiding calls (Friedmann 1955) and could conceivably be emitted by hungry fledglings (which are almost always abandoned by foster parents upon fledging – Short & Horne 2001), with some modification for the call needing to travel further distance, at inaccessible hives. By sitting at hives and begging, it is possible that the attention thus called of mammals able to break open the hive could initiate the process of associative learning described earlier, with the ontogeny of guiding developing via the food-associated mammals being begged to at ever-increasing distances from the bird's target hive (Friedmann 1955). An unresolved mystery affecting both hypotheses, however, is why the bird falls silent upon completing a guiding mission (Friedmann 1955; Isack 1987), when mobbing and begging tend to both increase in call volume with stimulus proximity.

Perhaps the area the emerges from the literature as being most under debate is *I.indicator*'s recruit targets. The details of reported targets are discussed later in 'Typical and Atypical Guiding Holotypes' but it is worth saying here that the only recruit known beyond doubt is *Homo sapiens*, perhaps the most advantageous partner possible to *I.indicator* for several reasons: as discussed previously, honeybee stings can be fatal to a honeyguide so recruiting a hive raider who can not only extract beecomb but, uniquely, also induce torpor in the bees via the aid of smoke is a valuable ally indeed. Humans are able negotiators of obstacles such as trees and rocks, are active at the same times of the day as honeyguides (daylight hours) and they also cement a strong relationship with *I.indicator* by very actively increasing their appeal to the bird as a target, termed 'valancy' by Russell 1935 (in Friedmann 1955), by advertising guiding willingness through whistles or other noises directed towards honeyguides in the area. *Homo heidelbergensis*, who was extant by 600 000 years bp, may have had a controlled use of fire, too (Bowman *et al* 2009), allowing it, and possibly earlier *Homo sapiens* ancestors, to have been effective prior raiding partners for *I.indicator* – a possibility that does not appear in honeyguide literature to date. In all these ways *Homo* emerges as a more ideal honeyguide partner than does the other main recruit target proposed: the honey badger, *Mellivora capensis* (often known as a 'ratel'). This medium-sized mustelid is partially nocturnal in much of its range, is a slightly less adept climber than humans, and does not seem to advertise its presence to honeyguides as much as honey-hunting humans do (Friedmann 1955; Short & Horne 2001, Begg 2006). Its one certain advantage as a potential recruit, however, is that, increasingly, it may be actively hunting for hives more than humans are in non-subsistence areas.

A final mystery in the evolution of *I.indicator*'s guiding is whether the bird has a known hive location in mind before the guiding mission commences, or whether it leads *ad hoc* to any hive it happens to come across while having a recruit in tow. Friedmann (1955) argues that, because of the usually circuitous and excessively long (50-130% longer than required – see **figure 3**) route described by the bird's guiding flight, it has no predetermined destination. Isack (1987), however, finds a complete contradiction to this in his mapping of guiding missions, with flights being remarkably direct, always arriving at the nearest hive in an area, and progressively guiding to the next furthest hive upon the first few being purposefully ignored by the human recruit. Importantly, he also notes a consistently-performed 'confirmation flight' at the outset of a guide, during which the bird flies away over the tree-line to appear a few minutes later after a duration which positively correlates with the distance of the target hive. This probable 'checking' of the spatial position of a previously known hive, along with *I.indicator*'s ceaseless habit of monitoring hives – which may be up to 13km apart (Isack 1987) – strongly suggests a set goal in the mind of the honeyguide, though expanding research in this area would be fascinating and informative.

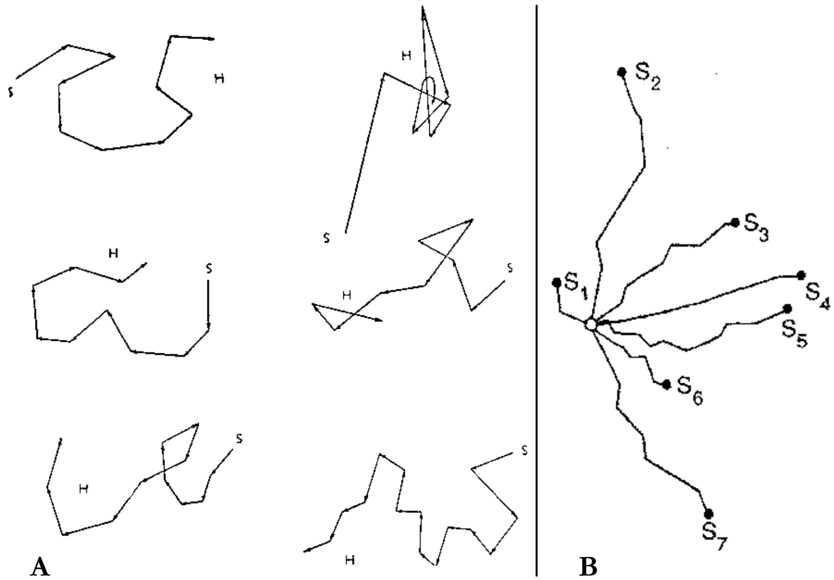


Figure 3 – Routes taken by *I.indicator* while guiding.

a) a typical collection of routes taken by different birds, as found by Friedmann (1955), showing 50-130% excess distance travelled ('S' denotes the guiding start point, 'H' denotes the hive location guided to); **b)** a set of routes taken to a single hive starting from different positions around the locality, as found by Isack & Reyer (1989), showing a generally linear route to the hive ('S' denotes the guiding start point).

Diagrams taken from Friedmann (1955) and Isack & Reyer (1989).

Typical and atypical guiding holotypes

As already stated, the only member of Indicatoridae known to guide for certain is the Greater, or 'Black-throated' Honeyguide, *Indicator indicator*. Therefore this section's collected observations relate to missions effected by it alone.

Typical Guiding:

The sequence of events constituting a typical guiding session, that occurring between *I.indicator* and a human honey-hunter, is illustrated in **figure 4**. It is almost always a lone, not necessarily hungry (Friedmann 1955) bird that initiates and conducts the guiding session, being particularly attracted by the sight of someone walking through the bush, sounds of people talking, the 'fuulido' whistle made by blowing into cupped fists, wood chopping sounds, livestock sounds, or the sight of smoke accompanied by human sounds. The 'search image' of the target seems relatively inexact, with women and young children (who rarely open wild bees' nests) being as likely to be accosted by the bird as are men, despite strongly gender-stereotyped dress prevailing in many guiding areas (Isack 1987). It is also not put off by large groups, with one recorded case in 1875 of a bird attempting to lead an entire cavalry squadron to a bees' nest (in Friedmann 1955).

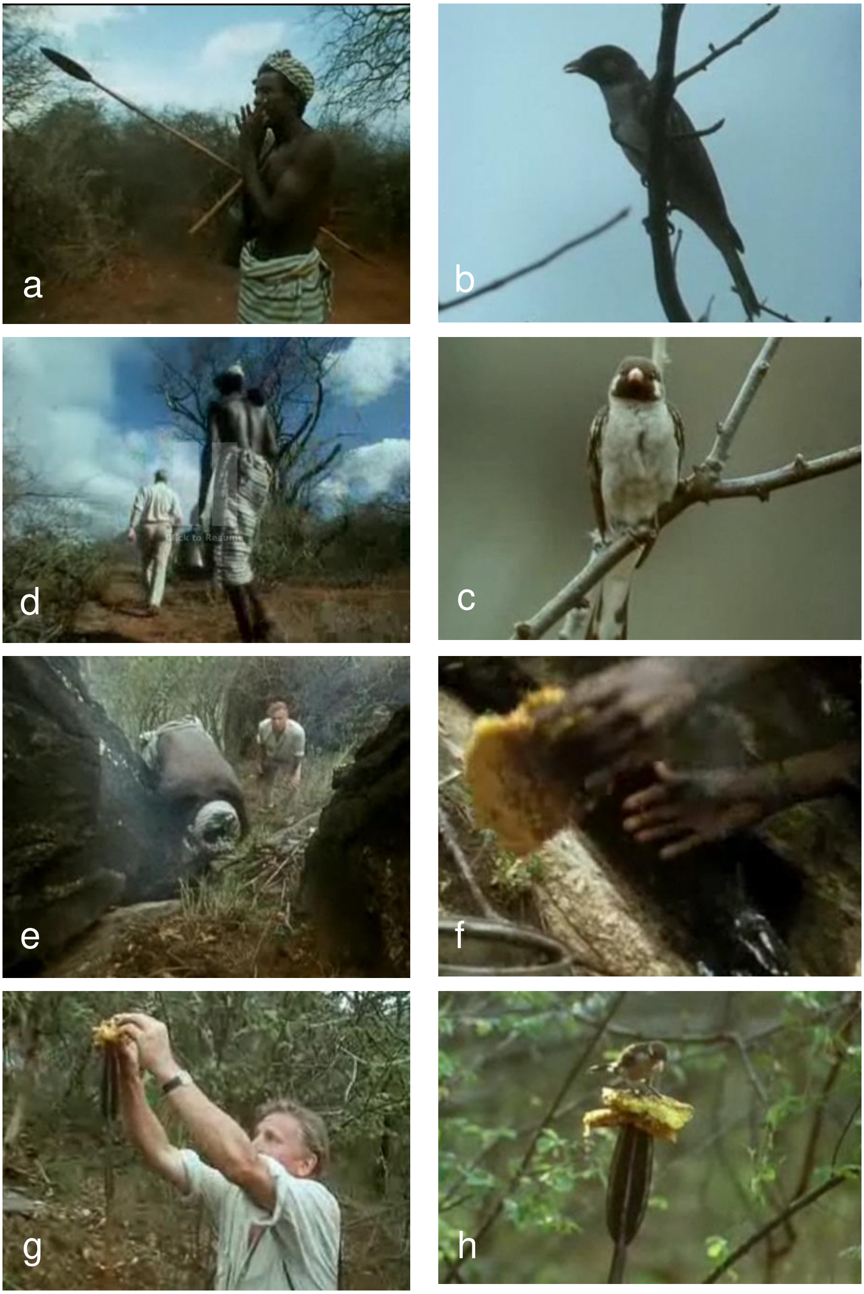

a
b
d
c
e
f
g
h

Figure 4, previous page – A typical guiding mission.

Photographic stills taken from BBC's *Trials of Life*, production details in **appendix 1**. **a)** a traditional Kenyan honey-hunter announces his presence to *I.indicator* by cupping his hands and blowing into them to make a whistles known as '*fuulido*'; **b)** a lone *I.indicator* (this one an adult) alights on a high branch nearby and begins making incessant chattering noises – the guiding call – to the human and flicking its distinctive white outer tail feathers; **c)** the bird flies roughly 20-50 metres away to a new perching place, still calling, with the honey-hunter and a young David Attenborough following it. It will make several of these pauses in the journey to allow the humans to catch up; **d)** the bird alights on a perching place nearer the ground and falls silent to indicate a hive has been reached; **e)** the bird's human partners use woodsmoke to induce the bees into torpor (low mobility); **f)** once the bees are quieter the honey-hunter reaches in and removes some bee comb; **g)** David eats a little comb and then leaves some for the bird as a reward for guiding them to it, as is commonly the Kenyan tradition; **h)** the bird partakes of its comb reward.

The guiding bird, most often an immature (though Skead 1951 and some correspondents in Friedmann 1955 disagree with this, and Friedmann 1955 notes that immature plumage can persist well into the bird's second year, so complicating age identification), upon beholding a target in an area with no already-opened hives, commences an excited call that sounds very much like someone frantically squeezing a dog's squeaky toy. Birds can be extremely persistent in trying to attract attention in this way, in some cases following an unresponsive human over 5 miles of terrain (Friedmann 1955) or chirring at them for a duration of up to 125 minutes (Isack 1987). Once a human target is engaged, the bird begins flying short intervals of roughly 50 metres between perching places, waiting for the recruit to catch up to around 5 metres away before flying to the next perching point (Skead 1951; Friedmann 1955; Macpherson 1975; Isack 1987; Isack & Reyer 1989; Short & Horne 2001). A guiding mission can cover a distance of as little as 200 metres and last under 8 minutes (Friedmann 1955), or range as far as 1 kilometre or more and last over 1 hour (Short & Horne 2001).

There is no discrimination by *I.indicator* as to whether terrain is traversable by its human partner (guiding over cliffs and gorges is not infrequent), whether dangerous animals in the human's path will prevent them from following, or whether a given hive will be accessible to a human any more than to itself (impregnable bees' nests inside rock fissures are sometimes led to) and unsatisfactory outcomes are not appreciably learnt from by the bird, who will persistently guide to the same rock fissure again and again (Isack 1987).

There is information on hive distance extractable from the flight pattern, with not only the duration of the initial confirmation flight being an indicator, but also with shorter distance between perching points indicating shorter distance to the hive (though perching height is not indicative of distance as many honey-hunters believe) (Isack 1987). Within 20 metres of the hive, the bird's calling becomes quieter and more intermittent until, upon reaching the hive location, the bird falls silent, finds a perching place near the hive and retreats into the foliage to observe the operation of the human raider(s) (Friedmann 1955; Isack 1987; Short & Horne 2001). A person ignoring or declining to open the first hive reached will usually elicit a second, third or fourth guide to the next nearest hive by the same impatient bird (Isack 1987).

The etiquette over whether to leave a honeyguide beecomb varies within and between human subsistence communities, with the majority of Boran tribe members of northern Kenya leaving the bird between 8g and 2.3kg of comb (*I.indicator* consumes roughly 15g of comb per day); however, a minority of Boran believe that the act of a female honeyguide eating a bee larva precipitates an 'immaculate conception', resulting in the 'pregnant' bird ceasing to guide and going into hiding to give birth instead. Since guiding is a desirable trait to honey-hunters, this situation is averted by the bird being rewarded not with comb but with honey solution (Isack 1987).

Seasonality in guiding is only slight or non-existent, with decreases in bee numbers in the dry season being apparently the only modifier (Friedmann 1955; Isack 1987). The behaviour can occur at any time in the day, though never at night when the birds are roosting; the only unresponsive times are when a bird is already feeding at an open hive, when a female is inspecting an avian host's nest-hole for the purposes of egg-laying, when a potential recruit target has remained unresponsive to the guiding call for more than 2 hours or when a male is at his territorial call post (Friedmann 1955; Isack 1987) – though Isack (1987) asserts that even this last activity can be interrupted if the bird knows of unopened hives in the locality.

Atypical Guiding:

Many reports of less usual guiding missions are recorded in Friedmann (1955) as information collected from various correspondents across Africa. Friedmann vetted these correspondents to determine their reliability, with the majority being amateur naturalists, zoological museum curators or long-time ranchers, all with fair ornithological experience. However, these are not empirical accounts and should be viewed as interesting observations on which future scientific study could be based, rather than being taken as authoritative themselves. Some reports of particular interest are reproduced below from Friedmann 1955, unless otherwise indicated as originating from another author.

Several correspondents report occasional instances of multiple birds guiding, though in Isack's (1987) experience these interlopers always chase off, or are chased off by, the original guide. This intolerance of supernumerary birds would not be surprising, since all members of *Indicator* compete aggressively at open hives (Short & Horne 2001).

So far in this report, only raids on, and guiding to, wild hives has been discussed; multiple correspondents, however, report frequent consumption by honeyguides of their own artificial hives – especially of the foundation wax – with guiding destinations occasionally being artificial hives too, though Skead (1951) reports only Lesser Honeyguides, *I.minor*, as being interested in his artificial hives. Other unusual guiding destinations include newly occupied bees' nest holes yet to have wax in them (suggesting the presence of bees as the honeyguide's hive location cue), hives in which the comb is already exposed (though Isack (1987) argues that on all occasions he has been guided to exposed comb the bees had yet to abscond, allowing honeyguides to still benefit from attracting smoke-using humans), comb-filled deserted wild hives or artificial hives with foundation wax present but bees not yet in residence (bringing into question bee presence as the sole cue used for locating hives, excepting in desertation cases where birds may remember previous occupation of a hive months in the past) and, finally, guiding missions leading not to a honeybee nest but to either honeybees feeding *en masse* from flowers or a honeybee-mimicking dipteran, *Philoliche magretti* (**figure 5**), which not only looks, sounds and moves like *Apis mellifera* but also congregates in swarms like it, too. Guiding to dipterans and foraging bees appears to reaffirm sensory cues based on the bees themselves as being important in hive-finding for honeyguides, and casts doubt upon the use of cues outside this; however, further research here would be informative – releasing honeybees mid-guide, for instance, may indicate their importance as a guide-halting mechanism. If it is a halting cue it is certainly a plastic one, since it is overridden in the situation mentioned in 'Typical Guiding' whereby birds can be induced to guide to successive hives by a human partner ignoring those arrived at.

Figure 5 – a *Philoliche* sp. bee mimic.

Many members of the genus *Philoliche*, in the family Tabanidae (horse-flies and allies), mimic bees in appearance, sound and behaviour. It is unknown whether members of the species shown here, *P.elongata*, are ever mistaken for honeybees, *Apis mellifera*, by honeyguides, but members of the sister species *P.magretti* occasionally are.

Image source: http://www.nzitrap.com/SiteMap.htm retrieved 18/4/2011.

Other less common targets for honeyguide raids, though not yet recorded as being guiding destinations, consist of the combs of both *Trigona* sweat bees (Short & Horne 2001) and wax-producing wasps (Isack 1987). Much has also been made, in both the popular literature and more obscure parts of the scientific literature, of *I.indicator* leading to danger; the popular literature (and local myths) assert that a previously unrewarded honeyguide will lead humans into the path of a dangerous animal as an act of revenge (Friedmann 1955; Isack 1987), whereas the scientific literature proposes the more sanguine hypothesis that the birds may become confused by the swarms of flies often surrounding large mammals (Layard 1869; Landrey 1925). In any case, no reliable reports exist of first-hand guidings to dangerous animals, and when Livingstone asked around 114 of his African assistants he found that only one had ever been led to anything other than a bees' nest, despite all having had some guiding experience (in Friedmann 1955).

Finally we come on to the most widely controversial aspect of *I.indicator*'s guiding: the recruit target. Occasional mention is made in the older literature of baboons, mongooses and monkeys (Friedmann 1955) as well as dogs (Layard 1869) being the (unresponsive) receivers of guiding initiation attempts. However, the real subject of the alternative mutualist debate is the honey badger or 'ratel', *Mellivora capensis* (**figure 6**). *I.indicator*'s formal describer, Andrew Sparrman, seems to have given the earliest in-print accounts of the ratel as a guiding partner, in the form of accounts collected from local East African people in 1785 (in Friedmann 1955). The relationship also permeates the beliefs of some tribes (e.g. the Hadza of Tanzania – Blench 2008) and can be found in their orally-transmitted legends. Modernly the concept has entered the popular imagination (for instance, see the Mimosa Films movie by Jamie Uys *Animals Are Beautiful People*, detailed in **appendix 1**, a tongue-in-cheek 'documentary' which apparently shows a wild ratel being led by *I.indicator*, which is in fact a tame ratel trained to follow a stuffed *I.indicator* on a fishing line – Mireschen Troskie-Marx, Mimosa Films, pers. comm. 2011 **[Erratum 2022: this statement was based on expert opinion, but has since been confirmed to me in personal communications as entirely correct by an original member of the production crew who wishes to remain anonymous]**). It has also entered the scientific literature despite no empirical evidence (e.g. Poche 1973; Fry 1988; Corning 1996). However, the pervasiveness of reports throughout *I.indicator* and *Mellivora capensis*' range overlap of a mutualism existing between the two (Friedmann 1955) hints at a possible basis in reality.

Figure 6 – The honey badger, *Mellivora capensis*.

Debate surrounds the theory that honey badgers are sometimes the guiding partners of the Greater Honeyguide. The pervasiveness of belief in the association amongst traditional honey-hunters across the African continent hints that there may be some truth to it, as these 'natural ethologists' have shown to be consistently reliable in their observations of other aspects of guiding (Isack & Reyer 1989).

Image source: http://honeybadger.anthonydeaver.com/ retrieved 18/4/2011.

Although Dean (1985), Dean, Siegfried and MacDonald (1990), and MacDonald (1994) have all claimed that the ratel is an unlikely partner due to its largely nocturnal habits and poor climbing ability (for accessing treetop hives), these objections have been disputed by Short & Horne (2001) who rather view the ratel's self-reliant hive-locating senses as a potential barrier to the mutualism arising. The ratel is known to have a foraging association with another bird – the Pale Chanting Goshawk, *Melierax canorus* (Guy 1971; Dean & MacDonald 1981; Steyn 1982; Borello & Borello 1986; Nelson & Nelson 1987; Paxton 1988) – and possibly with other mammals (Cooper 1976; Begg 2006) but despite ample opportunity for observation of the partnership, including by researchers working intensively on ratels in honeyguide range-overlap areas (Colleen Begg – pers. comm. 2011) it remains elusive. Yet, if willing human partners to *I.indicator* are in decline, the honey badger may become increasingly important to *I.indicator* if a relationship truly does exist and, if *I.indicator* is at all ecologically reliant on beecomb from inaccessible hives, these two species' fates may well be entwined.

Possible decline of guiding

The African continent is currently experiencing rapid socio-economic change in the form of higher wages, cheaper and improved schooling, greater availability of household goods and foodstuffs and wider access to modern medicines, all of which are creating a shift from historically pervasive hunter-gatherer and subsistence lifestyles to a mode of living in which personal foraging for food is de-emphasised. This change is observable even over such a short period as 7 years, with Isack (1987) finding, for instance, that in his Kenyan district of Marsabit 13 000 children attended primary schools in 1986 compared with only 4 400 in 1979. He also finds a change in equilibrium between the wages that can be earned by an adult male engaged in casual labour and the money that he can make by selling honey collected from the wild, with wages beginning to approximate the proceeds from honey vending in Kenya by 1986. An effect of this altered economic climate is to decrease interest in foraging for wild honey, since sugar is cheap and easy to get at local shops, medicines traditionally incorporating honey have been replaced by manufactured drugs and alcohol brewed from fermenting honey has been deemed unsafe compared to affordable alternatives and its production thus banned by governments (Isack 1987).

All this means that the services of the honeyguide are most likely in the lowest demand they've ever been by humans. Additionally, people who have historically had the closest contact with honeyguides are being encouraged or forced into new ways of life that decrease the reliance on wild foods; the numbers of herdsman and herdschildren, the most frequent targets of *I.indicator*'s guiding, are in decline, with herdsmen being in paid jobs and children being in school. An apparent effect of this is that knowledge of the guiding partnership between *I.indicator* and man is likewise in decline down the generations (found by Isack (1987) in interview with 960 local Kenyans). Interviews conducted with members of another Kenyan ethnic group, the Kikuyu, support this view, with few people under the age of 40 remembering a time when honeyguides were used to locate wild hives (Luca Borghesio – pers. comm. 2011). A segment of the human population that could have allayed this decline in Kenya is the Boran sub-community known as the 'Watt sub-group'. These traditional game hunters were frequent users of *I.indicator*'s guiding when looking for honey to sustain themselves on long hunts; however, with the arrival of Islam in the 19th century, the group began to become stigmatised and side-lined for the consumption of 'unclean' animals which made up a part of their catch. Laws introduced throughout the 1970s and 1980s in Kenya then forced the dwindling group to abandon their way of life altogether, for heavy restrictions on game-hunting and on damage to trees (sometimes necessary in accessing tree-dwelling honeybees' hives) made it untenable. All these social changes will, believes Isack, spell the end for the human-honeyguide mutualism, and with urban-edge birds ceasing to guide, the effect may already have begun (Friedmann 1955; Isack 1987).

In fact, JG Williams of Coryndon Natural History Museum in Nairobi, was already expressing concerns over guiding's decline to Herbert Friedmann in the 1950s, stating that, from his 'extensive' field experience, it appeared as though guiding had decreased over a period of 20 years or so and that inhabitants of Nairobi had told him they no longer considered wild honey as worthwhile collecting when sugar was so easily attainable (in Friedmann 1955). In the 1950s, too, the local idea that it was wrong to keep bees in artificial hives was beginning to be overturned, and the 1980s saw a rapid growth in ownership of artificial hives, supported by government subsidy, so that in Isack's district of Kenya the number jumped from 8 to more than 177 artificial hives in the period 1979-86 (Isack 1987).

Other experts, too, have expressed concern over a possible reduction in guiding's frequency (e.g. Queeny 1952; Short & Horne 2001) with some even recommending a program of 'behavioural conservation' by African park managers (Dean, Siegfried & MacDonald 1990). However, governments and wildlife organisations are understandably reluctant to put resources into such a program when there are other, more far-reaching wildlife concerns to be dealt with. Kabelo Senyatso of Birdlife Botswana explains that the approach conservation groups are needing to take is to prioritise the control of habitat degradation and modification, hunting, and poisoning; funding guiding preservation would divert resources from these larger concerns (pers. comm. 2011). As he says, "[it is questionable] whether behavioural conservation is as urgent an issue as ensuring the birds have habitats in which to live!" Honeyguide researcher Claire Spottiswoode agrees with this approach, believing it is better to preserve the bird than its guiding (Spottiswoode – pers. comm. 2011), and Short & Horne also warn of the importance of habitat threats to the bird, saying, " the pace of elimination of forests and woods tells us that we have little time before the number of threatened barbets, toucans and honeyguides increases." (Short & Horne 2001). Attention is also drawn by Short & Horne (2001) to suspicions that the 98% decrease in Kenya's forests in recent times is partly driven by the collusion of some government officials with illegal loggers, an effect which has dual importance to honeyguides, which are reliant on large old trees for providing homes to both honeybees and to potential hosts for the honeyguide's young.

I.indicator's numbers do not currently appear to be in radical decline. The IUCN, for instance, lists the species as 'Least Concern' (Birdlife International 2009) and Birdlife International's database of projected distributions shows only a change, not an increase or decrease, in *I.indicator*'s distribution (**figure 1a**); however, ornithologists with a good working knowledge of the bird's range and density do express concerns that population sizes are falling: in Malawi, the bird occupied 62% of atlas squares in the 2006 publication 'Birds of Malawi: an Atlas and Handbook', a figure the authors felt was reduced from previous years, which they attributed to diminishing stands of woodland (Dowsett-Lemaire & Dowsett 2006). Although any down-turn in *I.indicator* numbers would more likely be due to habitat loss than to the diminishing of guiding, it would still be well to understand the ecological interactions of this somewhat mysterious bird with the other organisms around it, since it is otherwise impossible to predict with any precision what the effect of population shifts in potential mutualists would have on *I.indicator*'s well-being. Conservation-stimulating research in this area could, of course, also benefit sympatric taxa, for which *I.indicator* may be well placed to serve as a charismatic representative in the process of seeking public funding.

A possible solution to the behavioural conservation dichotomy is one which relies on this public enthusiasm for *I.indicator* and its habits, though it is a measure heavily dependent on the goodwill of volunteers. In the

Ndoto Mountains of northern Kenya, Hussein Isack has set up a project which he hopes will protect the bird and its behaviour, using the skills of traditional honey-hunters to impart knowledge of guiding to younger generations:

> "We were able to organize for school children to accompany traditional honey hunters on honey hunting missions, to learn many survival skills and to form a 'young honey hunters club' – something close to 'Friends of the Honeyguide'!" [Isack – pers. comm. 2011]

If there continue to be people willing to invest their time in proffering this comradeship, it may turn out to be the only reasonable way in which *I.indicator*'s fascinating and scientifically challenging habits can be sustained.

Directions for Future Research

Four key areas have emerged from the presently-available literature to suggest themselves as being vital, or of interest, to study:

1) It is imperative that the relationship between honeyguides and other sympatric species be elucidated, with especial regard to potential non-human guiding targets (such as the honey badger, *Mellivora capensis*), and that the birds' level of dependence on any mutualist thus found be described.

2) There is a need to discern whether the loss of guiding in urban individuals of *I.indicator* can be regained in those individuals, since permanent disappearance of the behaviour may affect our willingness to conserve it.

3) Further study of the cues honeyguides use in detecting sources of wax would be of great scientific interest and would help resolve the current conflict in the literature as to whether the birds use olfaction as a detection method.

4) Investigation into the ontogeny of guiding behaviour would be useful in helping to inform our understanding of the evolutionary mechanisms involved in the formation of guiding behaviour, and may also provide insights into the evolution and stability of other, similar reciprocal service-providing mutualisms.

References

Achenbach A, Foitzik S (2009). 'First evidence for slave rebellion: enslaved ant workers systematically kill the brood of their social parasite Protomognathus americanus.' Evolution 63(4): 1068-1075.

Baird TA (1993). 'A new heterospecific foraging association between the puddingwife wrasse, Halichoeres radiatus, and the bar jack, Caranx ruber: evaluation of the foraging consequences.' Environmental Biology of Fishes 38: 393-397.

Begg CM (2006). 'Feeding ecology and social organisation of honey badgers (Mellivora capensis) in the southern Kalahari.' Thesis, available from University of Pretoria's Electronic Theses and Dissertations Service: http://upetd.up.ac.za/thesis/available/etd-11282005-145818/ – retrieved 3/1/2011.

BirdLife International 2009. Indicator indicator. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.3. <www.iucnredlist.org>. Retrieved 3/1/2011.

Blench RM (2008). 'Linguistic aspects of Hadza interactions with animals.' Unpublished manuscript, available from www.rogerblench.info – retrieved 3/1/2011.

Boesch C, Boesch H (1989). 'Hunting behavior of wild chimpanzees in the Taï National Park.' American Journal of Physical Anthropology 78: 547–573.

Borello W, Borello R (1986). 'Chanting Goshawks foraging with honey badger.' Babbler 12: 25.

Bowman DM, Balch JK, Artaxo P, DeFries S, Doyle JC, Harrison SP, Johnston FH, Keeley JE, Krawchuk MA, Kull CA, Marston JB, Moritz

MA, Prentice IC, Roos CI, Scott AC, Swetnam TW, van der Werf GR, Pyne SJ (2009). 'Fire in the Earth system.' Science 324: 481–4.

Bronstein, JL (1994). 'Our current understanding of mutualism.' Quarterly Review of Biology, 1: 31–51.

Bshary R, Hohner A, Ait-el-Djoudi K, Fricke H (2006). 'Interspecific Communicative and Coordinated Hunting between Groupers and Giant Moray Eels in the Red Sea.' PLoS Biology 4(12): e431.

Cooper RL (1976). 'Strange hunting companions.' Custos June/July: 42-44.

Corning PA (1996). 'The co-operative gene: on the role of synergy in evolution.' Evolutionary Theory 11: 183-207.

Dawson E, Chittka L (2010). 'The influence of conspecific and heterospecific cues on bumblebee foraging behaviour.' Association for the Study of Animal Behaviour Winter Meeting, Royal Zoological Society, London 2010.

Dean WRJ (1985). 'Greater Honeyguides and Ratels: how long will the myth continue?' Proc. Symp. Birds & Man, Johannesburg 1983: 217-223.

Dean WRJ, MacDonald IAW (1981). 'A review of African birds feeding in association with mammals.' Ostrich 52: 135-155.

Dean WRJ, Siegfried WR, MacDonald IAW (1990). ' The Fallacy, Fact, and Fate of Guiding Behavior in the Greater Honeyguide.' Conservation Biology 4(1): 99-101.

Devries PJ (1992). 'Singing Caterpillars, Ants and Symbiosis.' Scientific American 267(4): 76-82.

Diamond AW, Place AR (1988). 'Wax digestion by Black-throated Honey-guides Indicator indicator.' Ibis, 130: 558–561.

Diehl E, Junqueira LK, Berti-Filho E (2005). 'Ant and termite mound coinhabitants in the wetlands of Santo Antonio da Patrulha, Rio Grande do Sul, Brazil.' Brazilian Journal of Biology 65(3): 431-437.

Downs CT, van Dyk RJ, Iji P (2002). 'Wax digestion by the lesser honeyguide

Indicator minor.' Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology 133(1): 125-134.

Dowsett-Lemaire F, Dowsett RJ (2006). The Birds of Malawi: An Atlas and Handbook. Tauraco Press & Aves, Liège, Belgium.

Foster KR, Wenseleers T (2006). 'A general model for the evolution of mutualisms'. Journal of Evolutionary Biology 19: 1283-1293.

Friedmann H (1955). The Honeyguides. U. S. Nat. Mus. Bull. 208. Smithsonian Institute, Washington, D.C.

Friedmann H, Kern J (1956). 'The Problem of Cerophagy or Wax-Eating in the Honey-Guides.' The Quarterly Review of Biology 31(1): 19-30.

Fry CH (1977). 'Relation between mobbing and honey-guiding.' British Birds 70: 268-269.

Fry CH, Keith S, Urban EK (1988). The birds of Africa. Volume 3. Academic Press, London, England.

Graver A, Graver T, Otter K (2010). 'Interspecific communication in chickadees: do black-capped and mountain chickadees differentiate between each others chick-a-dee calls?' Association for the Study of Animal Behaviour Winter Meeting, Royal Zoological Society, London 2010.

Guy RD (1971). 'Goshawks, Ratels and wild honey.' African Wildlife 25: 53.

Hepburn HR (2010). 'Wax discrimination in the Lesser Honeyguide Indicator minor.' Ostrich 80(2): 119-120.

Herre EA, Knowlton N, Mueller UG, Rehner SA (1999). 'The evolution of mutualisms: exploring the paths between conflict and cooperation'. Trends in Ecology & Evolution 14: 49-53.

Hoesch W (1937). 'Ueber das "Honiganzeigen" von Indicator.' Journal of Ornithology 85(2): 201-205.

Horne JFM, Short LL (1990). 'Wax-eating by African Common Bulbuls.' Wilson Bulletin 102(2): 339-341.

Howell K (2009). 'Jenny Horne: In Appreciation of a Kenyan Mentor.' Journal of East African Natural History 98(1): 7-9.

Isack HA (1987). 'The biology of the Greater Honeyguide Indicator indicator: with emphasis on the guiding behaviour'. Thesis awarded by Oxford University, UK.

Isack HA, Reyer HU (1989). 'Honeyguides and honey gatherers: Interspecific communication in a symbiotic relationship.' Science 243(4896): 1343-1346.

Jacsó P (2004). 'Péter's digital ready reference shelf – Web of Knowledge', (web-only document), available at:

http://www.gale.cengage.com/servlet/HTMLFileServlet?imprint=9999&region=7&fileName=reference/archive/200408/webscience.html

retrieved 31/3/2011.

Jacsó P (2005). 'Savvy Searching – Google Scholar: the pros and the cons.' Online Information Review 29(2): 208-214.

Kostan KM (2002). 'The Evolution of Mutualistic Interspecific Communication: Assessment and Management Across Species.' Journal of Comparative Psychology 116(2): 206–209.

Landrey AG (1925). 'Do honey-guides lead to snakes?' The Blythswood Review 2(22): 66.

Layard EL (1869). 'Further Notes on South-African Ornithology.' Ibis 11: 361–378.

Macdonald I (1994). 'The Honeyguide and the honey badger: a persistent african fairy tale.' Africa – Environment & Wildlife 2(4) Pages unknown.

Macpherson DWK (1975). 'Deliberate guiding by the Greater Honeyguide.' Short notes - Ostrich 46: 186.

May RM (1989). 'Honeyguides and Humans.' News & Views: Nature 338: 707-708.

Mayr E (1956). Review of Friedmann's The Honeyguides. The Quarterly Review of Biology 31(4): 308-309.

McConnell PB, Baylis JR (1985). 'Interspecific Communication in Cooperative Herding: Acoustic and Visual Signals from Human Shepherds and Herding Dogs.' Zeitschrit für Tierpsychologie 67 (1-4): 302-328.

Mönkkönen M, Forsman JT, Helle P (1996). 'Mixed-Species Foraging Aggregations and Heterospecific Attraction in Boreal Bird Communities.' Oikos 77:1 127-136.

Moyer DC (1980). 'On Lesser Honeyguide and Black-collared Barbet.' Zambian Ornithological Society Newsletter 10: 159.

Murphy TG (2006). 'Predator-elicited visual signal: why the turquoise-browed motmot wag-displays its racketed tail.' Behavioral Ecology 17(4): 547-553.

Nakabachi A, Shigenobu S, Sakazume N, Shiraki T, Hayashizaki Y, Carninci P, Ishikawa H, Kudo T, Fukatsu T (2005). 'Transcriptome analysis of the aphid bacteriocyte, the symbiotic host cell that harbors an endocellular mutualistic bacterium, Buchnera.' Proceedings of the National Academy of Sciences of the United States of America 102(15): 5477-5482 .

Nelson R, Nelson J (1987). 'Observations of a honey badger and Chanting Goshawks at Nxai Pan.' Babbler 14: 18-19.

Ollerton J (2006). "Biological Barter": Patterns of Specialization Compared across Different Mutualisms. pp. 411-435 in: Waser NM & Ollerton J (Eds), Plant-Pollinator Interactions: From Specialization to Generalization. University of Chicago Press.

Ormond RFG (1980). 'Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators.' Journal of Zoology 191(2): 247-262.

Parker DA, Shulman MJ (1986). 'Avoiding predation: alarm responses of Caribbean sea urchins to simulated predation on conspecific and heterospecific sea urchins.' Marine Biology 93(2): 201-208.

Paxton M (1988). 'Foraging associations between Pale Chanting Goshawks, Honey Badgers and Slender Mongooses.' Gabar 3:82-84.

Pichersky E, Gershenzon J (2002). 'The formation and function of plant volatiles: perfumes for pollinator attraction and defense.' Current Opinion in Plant Biology 5: 237–243.

Place AR, Stiles EW (1992). 'Living off the wax of the land: Bayberries and Yellow-rumped Warblers.' The Auk 109: 334-345.

Poche R (1973). 'Niger's threatened Park W.' Oryx 12: 216-222.

Queeny EM (1952). 'The Wanderobo and the honey guide.' Natural History 61: 392-396.

Rothstein SI, Schreiber RW, Howell TR (1988). 'In Memoriam: Herbert Friedmann.' The Auk 105: 365-368.

Sharpe LL, Joustra AS, Cherry MI (2010). 'The presence of an avian co-forager reduces vigilance in a cooperative mammal.' Biology Letters 6(4): 475-477.

Short LL, Horne JFM (1990). 'Behavioural ecology of five sympatric Afrotropical honeyguides.' In Proceedings of International 100 Deutsche Ornithologische Gesellschaft Meeting, Current Topics in Avian Biology, Bonn, 1988 pp 319-325.

Short LL, Horne JFM (2001). Toucans, barbets and honeyguides: Ramphastidae, Capitonidae and Indicatoridae. Oxford University Press, Oxford.

Shropshire D (1931). 'The Bantu Conception of the Supra-mundane World.' Journal of the Royal African Society 30(118): 58-68.

Skead CJ (1951). 'Notes on Honeyguides in Southeast Cape Province, South Africa.' The Auk 68(1): 52-62.

Skinner BF (1966). 'The Phylogeny and Ontogeny of Behavior.' Science 153: 1205-1213.

Smith M (2011). Life With Birds. Whittles Publishing, Caithness, Scotland.

Spottiswoode CN, Colebrook-Robjent JFR (2007). ' Egg puncturing by the brood parasitic Greater Honeyguide and potential host counteradaptations.' Behavioural Ecology 18(4): 792-799.

Steyn P (1982). Birds of prey of southern Africa. David Phillip, Cape Town, South Africa.

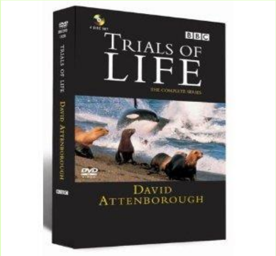
Strand S (1988). 'Following Behavior: Interspecific Foraging Associations among Gulf of California Reef Fishes.' Copeia 1988(2): 351-357.

Tinbergen L (1960). 'The natural control of insects in pinewoods.1. Factors influencing the intensity of predation by songbirds.' Archives Néerlandaises de Zoologie 13: 265-336.

von Frisch K (1967). The Dance Language and Orientation of Bees. Harvard University Press, Cambridge, Massachusetts.

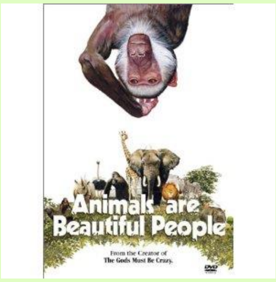
Wilson EO (1959). 'Communication by Tandem Running in the Ant Genus Cardiocondyla.' Psyche 66: 29-34.

Appendix 1 – Depictions of the Greater Honeyguide in the popular media



Episode 10: 'Talking to Strangers'. *The Trials of Life*. BBC, Bristol (1990). Originally aired 5 December 1990, BBC.

Wildlife documentary series showing, in episode 10, a guiding session by *Indicator indicator* with David Attenborough and a Kenyan honey-hunter as the recruits.

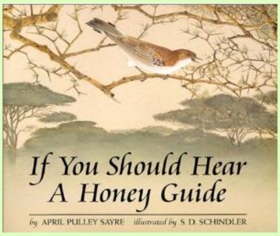


Uys J (Director) (1974). *Animals Are Beautiful People*. Mimosa Films, South Africa.

Tongue-in-cheek wildlife 'documentary' film, showing contrived situation of a honey badger being guided by (a stuffed) *Indicator indicator*.

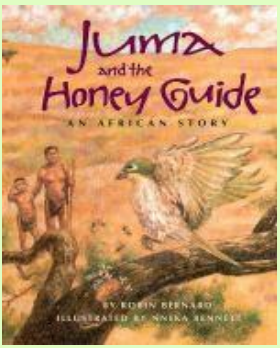
Episode 6: 'Grasslands: The Roots of Power'. *Human Planet*. BBC, Bristol (2011). Originally aired 17 February, BBC.

Documentary series on man's interaction with the natural world showing, in episode 6, guiding of humans by *Indicator indicator*. Incorrectly asserts the olfactory detection of wax hypothesis as fact.



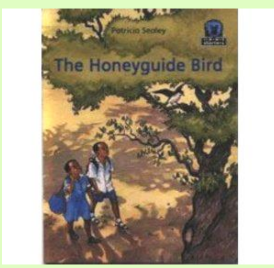
Pulley Sayre A (author), Schindler SD (illustrator) (1996). *If You Should Hear a Honey Guide*. Houghton Mifflin Juvenile Books, Boston, Massachusetts.

Illustrated childrens book which makes reference to *I.indicator*'s guiding habit.



Bernard R (author), Bennett N (illustrator) (1996). *Juma and the honeyguide: an African story*. Silver Burdett Press, New Jersey.

Illustrated childrens book which makes reference to *I.indicator*'s guiding habit.



Sealy P (1996). *The Honeyguide Bird (Junior African Writers: Starters Level 2)*. Heinemann, Portsmouth, New Hampshire.

Illustrated childrens book which makes reference to *I.indicator*'s guiding habit.

Appendix 2 – Where to access the honeyguide literature retrieved

Nb. The term 'fully available' is used here to indicate that both current issue and all back issues are available, unless stated otherwise. Memberships normally require a fee and paper copy back issues usually have an additional per item cost. Journals available electronically online are usually also available in paper copy from the publishing organisation.

Journal	Details
Africa - Environment & Wildlife	Renamed *Africa Geographic* in early 2000s, no back issues available before this date.
African Wildlife	The magazine of the Wildlife Society of South Africa (WESSA). Runs from 1946. Fully available to members in paper copy.
American Museum Novitates	Fully available free online at http://digitallibrary.amnh.org/dspace/handle/2246/9
American Naturalist	The journal of the American Society of Naturalists. Runs from 1867. Fully available to members online through JSTOR.
American Zoologist	Was the journal of the American Society of Zoologists, which became the Society for Integrative and Comparative Biology in 2002. Journal renamed to *Integrative and Comparative Biology* in the same year. Fully available to members online through JSTOR.
Annales du Musée Royal du Congo Belge, Tervuren, Zoologie	Not readily available in back issue, has undergone several name changes, though some volumes of several incarnations are available free online at the Biodiversity Heritage Library: http://www.biodiversitylibrary.org Journal home: http://www.africamuseum.be/museum/research/publications/rmca/journals/JAZ
Auk	The journal of the American Ornithologists' Union. Runs from 1884. Fully available to members online through JSTOR. Available free online up to 2001 from www.elibrary.unm.edu/sora/Auk

Aviculture Magazine	The magazine of The Aviculture Society. Runs from 1894. Fully available to members in paper copy.
Babbler	The journal of Birdlife Botswana. Runs from 1980. Available to members in paper copy only, with paper copy back-issues available from 1981-2008.
Bateleur	No modern presence.
Behavioral Ecology	Fully available to members online through Oxford Journals.
Blythswood Review	No modern presence.
Bokmakierie	The journal of the South African Ornithological Society. Ran 1948-89, then became 'Birding in southern Africa'. Not widely available in any format prior to name change.
British Birds	The magazine of the British Birds Charitable Trust. Fully available to members in paper copy.
Bulletin of the ABC (African Bird Club)	Runs from 1994. Fully available to members in paper copy.
Bulletin of the British Ornithologists' Club	Runs from 1892. Fully available to members in paper copy.
Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology	Fully available to members online through ScienceDirect (Elsevier).
Conservation Biology	Fully available to members online through JSTOR and Wiley Online Library.
Contributions in Science	An occasional publication by the Natural History Museum of Los Angeles County (formerly Los Angeles County Museum). Copies available free online back to 1973.
Durban Museum Novitates	Available to members in paper copy only, back issues run only as far back as 1997.
East African Natural History Society Bulletin	Only available in local (South and East African) libraries.
Honeyguide	The journal of Birdlife Zimbabwe, available in paper copy to members. Back issue availability unclear.

Ibis	The journal of the British Ornithologists' Union. Fully available to members online through Wiley Interscience
Journal of Comparative Psychology	A journal of the American Psychological Association. Formerly *Journal of Comparative and Physiological Psychology*. Fully available to members online through ScienceDirect (Elsevier).
Journal of Ornithology	The journal of the Deutsche Ornithologen-Gesellschaft (German Ornithologists' Society). Runs from 1853. Fully available to members through Springer.
Journal of the Bombay Natural History Society	Available to members in paper copy, limited back issues available on DVD.
Journal of the East Africa and Uganda Natural History Society	Renamed to *Journal of East African Natural History* in 1942. Runs from 1910. Fully available to members in paper copy and online through AJOL and BioOne.
Journal of the Royal African Society	Runs from 1901. Fully available to members online through JSTOR.
Journal of the South African Ornithologists' Union	No modern presence. First few issues (1905-1916) available free online at http://www.biodiversitylibrary.org/bibliography/8832
L'Apiculteur	No modern presence.
Living Bird	The magazine of the Cornell Lab of Ornithology. Available in paper copy only to members.
L'Oiseau	The magazine of France's Ligue pour la Protection des Oiseaux (League for the Protection of Birds). Fully available to members in paper copy.
Malimbus	The journal of the West African Ornithological Society. Available in paper form to members, free online up to 2005, and as pdfs on request for any back-issue later than 2005 for a fee.
Mitteilungen aus dem Zoologischen Museum in Berlin	Small number of early issues available free online at www.biodiversitylibrary.org/title/42540 otherwise no modern presence.
National Geographic Magazine	The journal of the National Geographic Society. Runs from 1888. Available to members in paper copy from National Geographic, back issues available on compilation DVDs.
Natural History	Formerly The American Museum Journal (1909-1918). Available in paper copy to members, back issue availability is unclear.

Nature	Fully available to members online through the Nature Publishing Group.
Ornithological Miscellany	No modern presence.
Oryx	The journal of conservation charity Fauna & Flora International. Fully available to members online through Cambridge University Press.
Ostrich	The journal of Birdlife South Africa. Fully available to members online through Informaworld.
Proceedings of the US National Museum	All available free online from http://www.biodiversitylibrary.org/bibliography/7519
Promerops	The magazine of the Cape Bird Club. Available to members in paper copy, availability of back issues unclear.
Quarterly Review of Biology	Fully available to members online through JSTOR.
Revue de Zoologie Africaine	Not readily available in back issue, has undergone several name changes, though some volumes of several incarnations are available free online at the Biodiversity Heritage Library: http://www.biodiversitylibrary.org Journal home: http://www.africamuseum.be/museum/research/publications/ rmca/journals/JAZ
Revue Zoologie de Afrique	Not readily available in back issue, has undergone several name changes, though some volumes of several incarnations are available free online at the Biodiversity Heritage Library: http://www.biodiversitylibrary.org Journal home: http://www.africamuseum.be/museum/research/publications/ rmca/journals/JAZ
Science	Fully available to members online through Science online.
Scopus	The journal of the East Africa Natural History Society. Runs from 1977. Fully available to members in paper copy.

Stray Feathers	Ran from 1872-1899. Founded by prominent ornithologist Allan Octavian Hume. Most issues available free online at http://www.biodiversitylibrary.org/bibliography/43405
Transactions of the Linnean Society of London	Ran 1791-1875, occasional issues available online free at http://en.wikisource.org/wiki/Transactions_of_the_Linnean_Society_of_London
Wilson Bulletin	Renamed *Wilson Journal of Ornithology* in 2006. The journal of the Wilson Ornithological Society (Michigan, US). Fully available free online at http://elibrary.unm.edu/sora/index.php
Yale Journal of Biology and Medicine	Fully available free online from PubMed Central.
Zambian Ornithological Society Newsletter	Available to members in paper copy, availability of back issues unclear.
Books made available online	
Friedmann, H (1955). The Honeyguides. U. S. Nat. Mus. Bull. 208. Smithsonian Institute, Washington, D.C.	Available in full free online from http://www.archive.org/stream/bulletinunitedst2081955unit/bulletinunitedst2081955unit_djvu.txt

Appendix 3 – All publications retrieved for the literature analysis and their database attributes.

Citation	Year	Journal	Journal 5 year impact factor ending 2007	Cited by	Accessibility rating	Has guiding as a main subject?	Has Greater Honey-guide as a main subject?
[Anonymous] (1956). 'African Honey-Guides' [editorial]. Science 123: 55.	1956	Science	30.631	29	4	Y	Y
*Archer AL, Glen RM (1969). 'Observations on the behaviour of two species of honey-guides Indicator variegatus (Lesson) and Indicator exilis (Cassin).' Contributions in Science, Natural History Museum of Los Angeles County 160: 1–6.	1969	Contributions In Science	0	6	2	N	N
Barneby WT (1900). 'Letter on the habits of the honey-guide.' Ibis ser 7 vol 6: 691-692	1900	Ibis	1.7	0	1	N	Y
Bates GL (1909). 'Melignomon robustus sp. n.' Bulletin of the British Ornithologists' Club 25: 26-27	1909	Bulletin of the British Ornithologists' Club	0	0	2	N	N
Begg ?M (2006). 'Feeding ecology and social organisation of honeybadgers (Mellivora capensis) in the southern Kalahari.' Thesis, available from University of Pretoria's Electronic Theses and Dissertations Service: http://upetd.up.ac.za/thesis/available/e	2006	N/A	N/A	0	5	N	N
Benson CW (1950). 'Parasitization of bee-eaters Meropidae by honey-guides, Indicator spp.' Ibis 92(3): 478-479.	1950	Ibis	1.7	0	2	N	Y
Berruti AB, McIntosh, Walter R (1995). 'Parasitism of the Blue Swallow Hirundo atrocaerulea by the Greater Honeyguide Indicator indicator.' Short Notes: Ostrich 66: 94.	1995	Ostrich	0.434	0	2	N	Y

Blench RM (2008). 'Linguistic aspects of Hadza interactions with animals.' Unpublished manuscript, available from www.rogerblench.info – retrieved 3/1/2011.	2008	N/A	N/A	0	5	N	N
Borello W, Borello R (1986). 'Chanting Goshawks foraging with honey badger.' Babbler 12: 25.	1986	Babbler	0	0	3	N	N
Bowden CGR, Hayman PV, Martins RP, Robertson PA, Mudd SH, Woodcock MW (1995). 'The Melignomon honeyguides: A review of recent range extensions and some remarks on their identification, with a description of the song of Zenker's Honeyguide.' Bulletin of	1995	Bulletin of the ABC (African Bird Club)	0	2	3	N	N
Brosset A (1981). 'Observation de l'Indicateur parasite prodotiscus insignis nourissant un jeune de son espèce.' L'Oiseau 51: 59-61.	1981	L'Oiseau	0	0	1	N	N
*Capkin B (1900). XLV – Letters, Extracts, Notices, &c. Ibis 42: 691–700.	1900	Ibis	1.7	0	3	N	Y
Chapin JP (1958). 'A new honey-guide from the Kivu District, Belgian Congo.' Bulletin of the British Ornithologists' Club 78: 46-48.	1958	Bulletin of the British Ornithologists' Club	0	0	2	N	N
Chapin JP (1962). 'Sibling Species Of Small African Honey-Guides.' Ibis 104: 40–44.	1962	Ibis	1.7	3	3	N	N
Chapin JP, Chapin RT, Short LL, Horne JFM (1987). 'Notes on the diet of the Least Honyguide Indicator exilis in eastern Zaire.' Bulletin of the British Ornithologists' Club 107: 32-35.	1987	Bulletin of the British Ornithologists' Club	0	0	2	N	N
Chiweshe NC, Dale J (2000). 'A merry-go-round story of a Greater Honeyguide.' Honeyguide 46(2): 167-169.	2000	Honeyguide	0	2	3	N	Y
Clancey PA (1979). 'The subspecies of the Scaly-throated Honeyguide Indicator variegatus (Lesson).' Durban Museum Novitates 12: 11-15.	1979	Durban Museum Novitates	0	0	1	N	N

Clancey PA (1985). 'On the East African races of the Scaly-throated Honeyguide.' Honeyguide 31: 101-103.	1985	Honeyguide	0	0	1	N	N
Colebrook-Robjent JFR, Stjernstedt R (1976). 'Chaplin's Barbet Lybius chaplini: first description of eggs, a new host record for the Lesser Honeyguide Indicator minor.' Bulletin of the British Ornithologists' Club 96: 109-111.	1976	Bulletin of the British Ornithologists' Club	0	0	2	N	N
Colston PR (1981). 'A newly described species of Melignomon (Indicatoridae) from Liberia, West Africa.' Bulletin of the British Ornithologists' Club 101: 289-291.	1981	Bulletin of the British Ornithologists' Club	0	0	2	N	N
Cronin R, Sherman PW (1977). 'A resource-based mating system: the Orange-rumped Honeyguide Indicator xanthonotus.' Living Bird 15: 5-37.	1977	Living Bird	0	0	1	N	N
Cunningham-van Someren GR (1970). 'On Prodotiscus insignis (Cassin) parasitizing Zosterops abyssinica (Guérin).' Bulletin of the British Ornithologists' Club 90: 129-131.	1970	Bulletin of the British Ornithologists' Club	0	0	2	N	N
*Cyrus D (1988). 'Observations on the parasitism of blackcollared barbets lybius-torquatus by the lesser honey-guide indicator-minor at lake-st-lucia-forest-station.' Ostrich 59(3): 138-139.	1988	Ostrich	0.434	0	2	N	N
Davey P (1994). 'Woodpecker feeding immature honeyguide.' Scopus 18: 61.	1994	Scopus	0	0	2	N	N
Dean WRJ (1985). 'Greater Honeyguides and Ratels: how long will the myth continue?' Proc. Symp. Birds & Man, Johannesburg 1983: 217-223.	1985	N/A	N/A	3	2	Y	Y
Dean WRJ, MacDonald IAW (1981). 'A review of African birds feeding in association with mammals.' Ostrich 52: 135-155.	1981	Ostrich	0.434	21	4	N	N
Dean WRJ, Siegfried WR, MacDonald IAW (1990). ' The Fallacy, Fact, and Fate of Guiding Behavior in the Greater Honeyguide.' Conservation Biology 4(1): 99-101.	1990	Conservation Biology	5.489	7	4	Y	Y

Diamond AW, Place AR (1988). 'Wax digestion by Black-throated Honey-guides Indicator indicator.' Ibis, 130: 558–561.	1988	Ibis	1.7	3	4	N	Y
Downs CT, van Dyk RJ, Iji P (2002). 'Wax digestion by the lesser honeyguide Indicator minor.' Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology 133(1): 125-134.	2002	Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology	1.983	4	4	N	N
Earlé RA, Herholdt JJ (1987). 'Notes on a Greater Honeyguide Indicator indicator chick raised by Anteating Chats Myrmecocichla formicivora.' Bulletin of the British Ornithologists' Club 107: 70-73.	1987	Bulletin of the British Ornithologists' Club	0	0	2	Y	Y
Finn F (1904). XXXV.—Letters, Extracts, Notices, &c. Ibis 46: 471–484.	1904	Ibis	1.7	0	4	N	Y
Friedmann H (1930). 'Notes on the sharp-billed honey-guide, Prodotiscus regulus.' Bateleur 2(4): 99-102.	1930	Bateleur	0	0	1	N	N
Friedmann H (1954). 'A revision of the classification of the honey-guides, Indicatoridae.' Annales du Musée Royal du Congo Belge, Tervuren, Zoologie 50: 21-27.	1954	Annales du Musée Royal du Congo Belge, Tervuren, Zoologie	0	0	1	N	Y
Friedmann H (1954). 'Honey-guide: The bird that eats wax.' National Geographic Magazine 105(4): 551-560, 8 plates.	1954	National Geographic Magazine	0	4	3	N	Y
Friedmann H (1957). 'Metabolic Aspects of Wax Digestion in Birds.' Yale Journal of Biology and Medicine 30(3): 244–247.	1957	Yale Journal of Biology and Medicine	0	0	2	N	Y
Friedmann H (1958). 'Advances in our knowledge of the honey-guides.' Proceedings of the U.S. National Museum 108: 309-320.	1958	Proceedings of the US National Museum	0	2	3	N	Y
Friedmann H (1963). 'Morphological data on two sibling species of small honey-guides.' Los Angeles County Museum, Contributions in Science 79.	1963	Contributions in Science	0	0	2	N	N
Friedmann H (1968). 'Additional data on brood parasitism in the honey-guides.' Proceedings of the U.S. National Museum 124: 1-8.	1968	Proceedings of the US National Museum	0	0	2	N	Y

Friedmann H (1968). 'Zenker's Honeyguide.' Journal of Ornithology 109(3): 276-283.	1968	Journal of Ornithology	1.459	1	4	N	N
Friedmann H (1970). 'Further information on the breeding biology of the honey-guides.' Los Angeles County Museum, Contributions in Science 205	1970	Contributions in Science	0	0	2	N	Y
Friedmann H (1971). 'Phenotypic potential and speciation in Indicator and Prodotiscus.' Ostrich 8 (suppl.): 21-26.	1971	Ostrich	0.434	0	2	N	N
Friedmann H (1976). 'The Asian honeyguides.' Journal of the Bombay Natural History Society 71: 426-432.	1976	Journal of the Bombay Natural History Society	0	0	2	N	N
Friedmann H (1978). 'Current knowledge of the Lyre-tailed Honey-guide, Melichneutes robustus (Bates) and its implications (Aves Indicatoridae).' Revue de Zoologie Afrìcaine 92: 644-656	1978	Revue de Zoologie Africaine	0	0	1	N	N
Friedmann H, Kern J (1956). 'The Problem of Cerophagy or Wax-Eating in the Honey-Guides.' The Quarterly Review of Biology 31(1): 19-30.	1956	Quarterly Review of Biology	7.476	17	4	N	Y
Friedmann H, Kern J, Rust J (1957). 'The Domestic Chick: A Substitute for the Honey-guide as a Symbiont with Cerolytic Microorganisms.' The American Naturalist 91(860): 321-325.	1957	American Naturalist	5.605	3	4	N	N
Friedmann, H (1955). The Honeyguides. U. S. Nat. Mus. Bull. 208. Smithsonian Institute, Washington, D.C.	1955	N/A	N/A	62	3	Y	Y
Fry CH (1977). 'Relation between mobbing and honey-guiding.' British Birds 70: 268-269.	1977	British Birds	0	0	2	Y	Y
Gardiner N (1975). 'Striped Kingfisher as host to Greater Honey-guide.' East African Natural History Society Bulletin Aug/Sep. 1975 p89.	1975	East African Natural History Society Bulletin	0	0	1	N	Y
Gilges W (1939). 'A contribution to the habits of the honeyguide.' Ostrich 10(2): 130-133, figs. 1, 2.	1939	Ostrich	0.434	0	2	N	Y
Godfrey R (1925). 'Honeyguides'. The Blythswood Review 2(17): 43.	1925	Blythswood Review	0	0	1	N	Y

Guy RD (1971). 'Goshawks, Ratels and wild honey.' African Wildlife 25: 53.	1971	African Wildlife	0	0	2	N	N
Haagner AK (1907). 'A contribution to our knowledge of the Indicatoridae (honey-guides).' Journal of the South African Ornithologists' Union ser. 2, 1, 1-5.	1907	Journal of the South African Ornithologists' Union	0	0	1	N	Y
Haagner AK (1911). 'A further note on the mandibular hook of the honey-guide.' Journal of the South African Ornithologists' Union ser. 2, 7, 79.	1911	Journal of the South African Ornithologists' Union	0	0	1	N	Y
Hepburn HR (2010). 'Wax discrimination in the Lesser Honeyguide Indicator minor.' Ostrich 80(2): 119-120.	2010	Ostrich	0.434	1	4	N	N
Hoesch W (1937). 'Ueber das "Honiganzeigen" von Indicator.' Journal of Ornithology 85(2): 201-205.	1937	Journal of Ornithology	1.459	0	4	N	Y
Horne JFM, Short LL (1990). 'Wax-eating by African Common Bulbuls.' Wilson Bulletin 102(2): 339-341.	1990	Wilson Bulletin	0.719	0	4	N	N
Hosken JH (1966). 'Sharp-billed Honeyguide Prodotiscus regulus being fed by a pair of Cisticolas.' Ostrich 37(4): 235.	1966	Ostrich	0.434	0	2	N	N
Hume AO (1873). 'Notes. Indicator xanthonotus'. Stray Feathers 1: 313-315.	1873	Stray Feathers	0	0	2	N	N
Hussain SA (1978). 'Orange-rumped Honeyguide (Indicator xanthonotus) in the Garhwal Himalayas.' Journal of the Bombay Natural History Society 75: 487-488.	1978	Journal of the Bombay Natural History Society	0	0	2	N	N
Hussain SA, Ali S (1983). 'Some notes on the ecology and status of the Orange-rumped Honeyguide Indicator xanthonotus in the Himalayas.' Journal of the Bombay Natural History Society 80: 564-574.	1983	Journal of the Bombay Natural History Society	0	0	2	N	N
*Isack HA (1986). 'The Greater Honeyguide dilemma.' Acta XIX Congressus Internationalis Ornithologici 2: 2,768-2,780.	1986	N/A	N/A	0	1	Y	Y

Isack HA (1987). 'The biology of the Greater Honeyguide Indicator indicator: with emphasis on the guiding behaviour'. Thesis awarded by Oxford University, UK.	1987	N/A	N/A	0	2	Y	Y
Isack HA, Reyer HU (1989). 'Honeyguides and honey gatherers: Interspecific communication in a symbiotic relationship.' Science 243(4896): 1343-1346.	1989	Science	30.631	38	5	Y	Y
Jackson FJ (1913). 'On honey guides.' Journal of the East Africa and Uganda Natural History Society 4(7): 78-79.	1913	Journal of the East Africa and Uganda Natural History Society	0	0	2	N	Y
Jeffreys MDW (1951). 'An Early Reference To The Lesser Honey-guide.' Ibis 93: 626.	1951	Ibis	1.7	0	4	N	N
Johnsgard PA (1997). The Avian Brood Parasites. Oxford University Press, Oxford.	1997	N/A	N/A	62	3	N	N
Jubb RA (1966). 'Red-billed Hoopoe and a greater Honey-guide.' Bokmakierie 18: 66.	1966	Bokmakierie	0	4	1	N	Y
Kostan KM (2002). 'The Evolution of Mutualistic Interspecific Communication: Assessment and Management Across Species.' Journal of Comparative Psychology 116(2): 206–209.	2002	Journal of Comparative Psychology	1.825	7	4	N	N
Landrey AG (1925). 'Do honey-guides lead to snakes?' The Blythswood Review 2(22): 66.	1925	Blythswood Review	0	0	1	Y	Y
Layard EL (1869). 'Further Notes on South-African Ornithology.' Ibis 11: 361–378.	1869	Ibis	1.7	2	4	N	N
Leadbeater B (1833). 'Descriptions of some new species of birds belonging chiefly to the rare genera Phytotoma, Gmel., Indicator, Vieill., and Cursorius, Latham.' Transactions of the Linnean Society of London 16: 85-93	1833	Transactions of the Linnean Society of London	0	0	1	N	N

Louette M (1981). 'A new species of honeyguide from West Africa.' Revue Zoologie de Afrique Volume and page numbers unknown	1981	Revue Zoologie de Afrique	0	4	1	N	N
Lowe PR (1946). 'On the systematic position of the woodpeckers (Pici), honey-guides (Indicator), hoopoes and others.' Ibis 88: 103-127, 15 figs	1946	Ibis	1.7	0	4	N	N
Lowther PE (2007). 'Host list of avian brood parasites - 4 - Piciformes; Indicatoridae.' The Field Museum website. Version: 5 August 2007. Available from: http://fm1.fieldmuseum.org/aa/Files/lowther/IList.pdf – retrieved 4/1/2011.	2007	N/A	N/A	0	5	N	N
Macdonald I (1994). 'The Honeyguide and the honey badger: a persistent african fairy tale.' Africa – Environment & Wildlife 2(4) Pages unknown.	1994	Africa - Environment & Wildlife	0	0	1	Y	Y
Macpherson DWK (1975). 'Deliberate guiding by the Greater Honeyguide.' Short notes - Ostrich 46: 186.	1975	Ostrich	0.434	0	2	Y	Y
Madge SG, Cunnigham-van Someren (1975). 'Black-throated Honeyguide and Abyssinian Scimitar-bills.' East African Natural History Society Bulletin Dec. 1975 pp130-131.	1975	East African Natural History Society Bulletin	0	0	1	N	Y
Marchant S (1950). 'A new race of honey-guide...from Nigeria.' Bulletin of the British Ornithologists' Club 70(3): 25-26.	1950	Bulletin of the British Ornithologists' Club	0	0	2	N	N
May RM (1989). 'Honeyguides and Humans.' News & Views: Nature 338: 707-708.	1989	Nature	30.616	0	5	Y	Y
Mayr E (1956). Review of Friedmann's The Honeyguides. The Quarterly Review of Biology 31(4): 308-309.	1956	Quarterly Review of Biology	7.476	0	4	N	Y
Moyer DC (1980). (On Lesser Honeyguide and Black-collared Barbet). Zambian Ornithological Society Newsletter 10: 159.	1980	Zambian Ornithological Society Newsletter	0	0	1	N	N
Patten GH (1952). 'A greater honeyguide chick.' Bokmakierie 4(2): 42	1952	Bokmakierie	0	0	1	N	Y

Payne RB (1992). 'Clutch size, laying periodicity and behaviour in the honeyguides Indicator indicator and I. minor.' Proceedings of the VII Pan-African Ornithological Congress 537-547.	1992	N/A	N/A	0	1	N	Y
Pillain A (1873). 'Les oiseaux melitophages. Les indicateurs.' L'Apiculteur 17: 214-216.	1873	L'Apiculteur	0	0	1	N	Y
Place AR, Duke G, Jackson S, Roby D (1990). 'The problem of cerophagy – revisited.' Acta XX Congressus Internationalis Ornithologici Supplement p514.	1990	N/A	N/A	0	1	N	N
Plowes DCH (1948). 'Nesting of the Greater Honeyguide.' Ostrich 19:171-172.	1948	Ostrich	0.434	0	2	N	Y
Poche R (1973). 'Niger's threatened Park W.' Oryx 12: 216-222.	1973	Oryx	1.647	11	4	N	N
Porter S (1927). 'A tame honey-guide.' Aviculture Magazine (ser 4) 5: 152-155.	1927	Aviculture Magazine	0	0	2	N	Y
Priest CD (1931). 'Foster parent of a honeyguide?' Ostrich 2(2): 66-67.	1931	Ostrich	0.434	0	2	N	N
Queeny EM (1952). 'The Wanderobo and the honey guide.' Natural History 61: 392-396, 10 plates.	1952	Natural History	0.059	3	3	Y	Y
Rainey H, Borrow N, Demey R, Fishpool LDC (2003). 'First recordings of vocalisations of Yellow-footed Honeyguide Melignomon eisentrauti and confirmed records in Ivory Coast.' Malimbus 25: 31-38.	2003	Malimbus	0	1	5	N	N
Ranger GA (1955). 'On Three Species of Honey-guide; the Greater (Indicator indicator); the Lesser (Indicator minor) and the Scaly-Throated (Indicator variegatus).' Ostrich 26(2): 70-87.	1955	Ostrich	0.434	5	4	N	Y
Roberts A (1930). 'The sharp-billed honeyguide.' Bateleur 2(2): 39-41	1930	Bateleur	0	0	1	N	N

Roberts HA (1956). 'Breeding tactics of the two honey-guides – Indicator indicator (Sparrman) and Indicator minor (Stephens).' Bulletin of the British Ornithologists' Club 76:114.	1956	Bulletin of the British Ornithologists' Club	0	0	2	N	Y
Roberts WW (1925). 'Honey-guides.' The Blythswood Review 2(17): 43	1925	Blythswood Review	0	0	1	N	Y
Rougeot PC (1950). 'Contribution à l'étude des indicatoridés de la foret Gabonaise.' L'Oiseau 20(1): 51-63	1950	L'Oiseau	0	0	2	N	N
Rougeot PC (1951). 'Nouvelles observations sur le Melichneutes robustus (Bates).' L'Oíseau 21: 127-134.	1951	L'Oiseau	0	0	2	N	N
Rougeot PC (1959). 'Notes biologiques sur l'indicateur a queue en lyre: Melichneutes robustus (Bates).' Ostrich Supplement 3: 271-273.	1959	Ostrich	0.434	0	2	N	N
Sclater PL (1870). 'Note on the systematic position of Indicator.' Ibis (ser 2) 6: 176-189, 2 figs.	1870	Ibis	1.7	0	4	N	N
Serle W (1959). 'Note on the immature plumage of the honey-guide Melignomon zenkeri Reichenow.' Bulletin of the British Ornithlogists' Club (Vol and pp unknown).	1959	Bulletin of the British Ornithologists' Club	0	2	3	N	N
Sharpe RB (1876). 'A revision of the family Indicatoridae' in Rowley, Ornithological Miscellany 1(3):192-209, 1 plate.	1976	Ornithological Miscellany	0	0	1	N	Y
Short LL, Horne JFM (1979). 'Vocal display and some interactions of Kenyan honeyguides (Indicatoridae) with barbets (Capitonidae).' American Museum Novitates 2684.	1979	American Museum Novitates	1.635	0	2	N	Y
Short LL, Horne JFM (1983). 'The relationship of male Lesser Honeyguides Indicator minor with duetting barbet pairs.' Bulletin of the British Ornithologists' Club 103: 25-32.	1983	Bulletin of the British Ornithologists' Club	0	0	2	N	N
Short LL, Horne JFM (1985). 'Behavioral notes on the nest-parasitic Afrotropical honeyguides (Aves: Indicatoridae).' American Museum Novitates 2825.	1985	American Museum Novitates	1.635	7	3	N	Y

Short LL, Horne JFM (1988a). 'Indicatoridae, honeyguides.' in The Birds of Africa, vol. 3. (eds. CH Fry, S Keith and EK Urban), pp 486-512. Academic Press, London, UK.	1988	N/A	N/A	0	3	N	Y
Short LL, Horne JFM (1988b). 'Lesser Honeyguide Indicator minor interactions with its barbet hosts.' In Proceedings of the Sixth Pan-African Ornithological Congress pp 65-75.	1988	N/A	N/A	0	1	N	N
Short LL, Horne JFM (1990). 'Behavioural ecology of five sympatric Afrotropical honeyguides.' In Proceedings of International 100 Deutsche Ornithologische Gesellschaft Meeting, Current Topics in Avian Biology, Bonn, 1988 pp 319-325.	1990	N/A	N/A	0	1	Y	Y
Short LL, Horne JFM (1992). Bird family profiles. 1: Honeyguides. Kenya Birds 1: 6-7.	1992	N/A	N/A	0	2	N	Y
Short LL, Horne JFM (1992). 'Honeyguide–host interactions.' In Proceedings of the VII Pan-African Ornithological Congress pp 549-552.	1992	N/A	N/A	0	1	N	Y
Short LL, Horne JFM (2001). Toucans, barbets and honeyguides: Ramphastidae, Capitonidae and Indicatoridae. Oxford University Press, Oxford.	2001	N/A	N/A	9	4	N	Y
Short LL, Horne JFM (2002). 'Family Indicatoridae (Honeyguides)' pp. 274-295 in del Hoyo J, Elliott A, Sargatal J, (editors), Handbook of the Birds of the World. Vol. 7. Lynx Edicions, Barcelona, Spain.	2002	N/A	N/A	0	4	N	Y
Short LL, Horne JFM, Chapin JP (1987). 'Indicator narokensis Jackson is synonym of Indicator meliphilus (Oberholser).' Mitteilungen aus dem Zoologischen Museum in Berlin 63 (Annalen für Ornithologie 11): 161-168.	1987	Mitteilungen aus dem Zoologischen Museum in Berlin	0	0	1	N	N
Shropshire D (1931). 'The Bantu Conception of the Supra-mundane World.' Journal of the Royal African Society 30(118): 58-68.	1931	Journal of the Royal African Society	0	1	4	N	N

Skead CJ (1946). 'Hive indication by the greater honeyguide.' Ostrich 17(3): 199-201, 1 fig.	1946	Ostrich	0.434	0	2	Y	Y
Skead CJ (1950). 'A study of the black-collared barbet, Lybius torquaus with notes on its parasitism by the lesser honeyguide, Indicator minor.' Ostrich 21: 84-96.	1950	Ostrich	0.434	6	4	N	N
Skead CJ (1951). 'Notes on Honeyguides in Southeast Cape Province, South Africa.' The Auk 68(1): 52-62.	1951	Auk	2.709	7	4	Y	Y
Spottiswoode CN (1994). 'Lesser Honeyguide parasitizing Cardinal Woodpecker.' Promerops 213: 9.	1994	Promerops	0	0	1	N	N
Spottiswoode CN, Colebrook-Robjent JFR (2007). ' Egg puncturing by the brood parasitic Greater Honeyguide and potential host counteradaptations.' Behavioural Ecology 18(4): 792-799.	2007	Behavioral Ecology	3.54	6	5	N	Y
*Stager KE (1967). 'Avian olfaction.' American Zoologist 7: 415–420.	1967	American Zoologist	3.274	34	4	N	Y
Stoliczka F (1873). 'Letter on anatomy of Indicator xanthonotus.' Stray Feathers 1: 425-427.	1873	Stray Feathers	0	0	2	N	N
Underhill LG, Underhill GD, Martin CGC, Fraser MW (1995). 'Primary moult, wing-length and mass of the Lesser Honeyguide Indicator minor.' Bulletin of the British Ornithologists' Club 115: 229-234.	1995	Bulletin of the British Ornithologists' Club	0	0	2	N	N
Vernon CJ (1987a). 'On the Eastern Green-backed Honeyguide.' Honeyguide 33: 6-12.	1987	Honeyguide	0	0	3	N	N
Vernon CJ (1987b). 'Bill hooks of Prodotiscus nestlings.' Ostrich 58: 187.	1987	Ostrich	0.434	0	2	N	N
Williams JG (1965). 'The pygmy honey-guide, Indicator pumilio Chapin in East Africa.' Bulletin of the British Ornithologists' Club 85 (Pp unknown).	1965	Bulletin of the British Ornithologists' Club	0	2	3	N	N
Wood RC (1940). ''Drumming' of the Black-throated Honeyguide (Indicator indicator).' Ostrich 11: 50-51.	1940	Ostrich	0.434	0	2	N	Y
* denotes a publication recovered after the literature analysis, thus omitted from charts and discussion. 5 omitted records + 120 included records = 125 records in total.							